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SAST – Hawksbill turtle – 5,31(07)017,01

SYNOPSIS OF BIOLOGICAL DATA ON THE HAWKSBILL TURTLE *Eretmochelys imbricata* (Linnaeus, 1766)

Prepared by
W.N. Witzell

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FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

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SAST - Hawksbill turtle - 5,31 (07) 017,01

SYNOPSIS OF BIOLOGICAL DATA ON THE HAWKSBILL TURTLE

Eretmochelys imbricata (Linnaeus, 1766)

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PREPARATION OF THIS SYNOPSIS

This review is the first attempt to collate and synopsize the existing fragments of hawksbill data which are scattered throughout a myriad of published and unpublished reports. In order to address all pertinent categories of data, this review follows the FAO species synopsis format prepared by Rosa, Jr. (1965).

The hawksbill sea turtle has been harvested for centuries for its meat and its beautiful mottled carapace scutes, called "tortoise shell". However, hawksbills appear to be dwindling rapidly over much of their range due to overexploitation and habitat destruction. The world-wide scientific and conservation community has therefore declared the hawksbill an endangered species.

The basic biology and population dynamics of the hawksbill turtle, needed by resource managers, is poorly understood. The hawksbill is an elusive animal, diffusely nesting over extended nesting seasons on scattered tropical beaches throughout its range. They may be ubiquitous in shallow waters surrounding tropical reefs but are not often seen, and the females are generally very rapid nesters, making them difficult to study. They are opportunistic omnivores with little apparent tendency to migrate great distances en masse. Also, the hawksbill turtle, unlike many marine vertebrates, apparently consists of many separate populations that mate and nest independently at site specific locations. These factors combined illustrate the complexity of formulating rational management strategies.

ABSTRACT

This synopsis compiles and reviews the scattered information on the identity, distribution, life history, populations, exploitation, protection, management and mariculture potential of the hawksbill turtle, Eretmochelys imbricata (Linnaeus, 1766), harvested for centuries for its meat and carapace scutes.

Distribution

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1/ No information available

1. IDENTITY

1.1 Nomenclature

1.1.1 Valid name

Eretmochelys imbricata (Linnaeus, 1766)

1.1.2 Synonymy (modified from Deraniyagala, 1939; Mertens and Wermuth, 1955; Loveridge and Williams, 1957; and Wermuth and Mertens, 1961)

Testudo imbricata Linnaeus, Syst. Nat., ed. 12, 1766, p. 350: American and Asiatic Seas (restricted to Bermuda Islands by Smith and Taylor, Univ. Kansas Sci. Bull. 1950a. 33(II) (8):315)

Chelonia imbricata Schweigger, Prodr. Mon. Chel., 1812, p. 291

Caretta imbricata Merrem, Syst. Amph. 1820, p. 19

Chelonia pseudo-mydas Lesson, In Belanger, Voy. Indies-Orient., Zool., 1834, p. 299: Atlantic Ocean (restricted to Bermuda Islands by Smith and Taylor, Bull. U.S. Natl. Mus. 1950b. 199:16)

Chelonia pseudo-caretta Lesson, In Belanger, Voy. Indies-Orient., Zool., 1834, p. 302: Atlantic Ocean (restricted to Bermuda Islands by Smith and Taylor, Bull. U.S. Natl. Mus. 1950b. 199:16)

Caretta bissa Rüppell, Neue Wirbelth. Fauna Abyss., Amphib., 1835, p. 4, pl. ii: Red Sea

Eretmochelys imbricata Fitzinger, Syst. Rept. 1843, p. 30: American Seas (restricted to Bermuda Islands by Smith and Taylor, Bull. U.S. Natl. Mus. 1950b. 199:17)

Eretmochelys squamata Agassiz, Contr. Nat. Hist. Mus. U.S., 1, 1857, p. 382: Indian and Pacific oceans (restricted to Singapore, Straits Settlements by Smith and Taylor, Bull. U.S. Natl. Mus. 1950a. 199:17)

Caretta squamosa Girard, U.S. Explor. Exped. 1838-1842, Herp., 1858, p. 442, pl. xxx, Figures 1-7: Sulu Seas and Indian Ocean

Caretta rostrata Girard, U.S. Explor. Exped. 1838-1842, Herp., 1858, p. 446, pl. xxx, Figures 8-13: Fiji Islands

Chelone imbricata Strauch, Chelon. Stud., 1862, p. 181

Onchochelys kraussi Gray, Proc. Zool. Soc. Lond., 1873, p. 398, Figures 1-2: Atlantic Ocean off French Guyana

Ahrenfeldt (1954) provided an early synonymy and discussed the confusion caused by Linnaeus who apparently misnamed the hawksbill Testudo instead of the more appropriate Caretta.

1.2 Taxonomy

1.2.1 Affinities

- Suprageneric

Phylum Chordata
Subphylum Vertebrata
Superclass Tetropoda
Class Reptilia
Subclass Anapsida
Order Testudinata
Suborder Cryptodira
Superfamily Chelonioidae
Family Cheloniidae

- Generic Eretmochelys (from Loveridge and Williams, 1957)

Caretta Ritgen (not of Rafinesque: 1814) 1828: Nova Acta Acad. Leop. Carol. 14, p. 270. Type: Testudo imbricata Linnaeus (by monotypy)

Eretmochelys Fitzinger, 1843: Syst. Rept., p. 30. Type: T. imbricata Linnaeus (by monotypy)

Herpysmostes Gistel 1868: Die Lurche Europa, p. 145. Type: T. imbricata Linnaeus (fide Mertens, 1936: Senckenbergiana, 18, p. 75)

Onychochelys Gray, 1873: Proc. Zool. Soc. Lond., p. 397, Figures 1-2. Type: O. kraussi Gray = T. imbricata Linnaeus (by monotypy)

- Generic

Genus Eretmochelys monotypic, see specific diagnosis.

- Specific

Diagnosis: two pairs of prefrontal scales; dorsal scutes conspicuously imbricate (except in very young or very old turtles); four pairs of lateral scutes, anterior pair not touching precentral scute; two claws on each flipper; head compressed; mouth beak-like (Figure 1). Detailed descriptions are found in Taylor (1921, 1970), Deraniyagala (1930, 1939), Le Poulain (1941), Bourret (1941), Carr (1942), Loveridge and Williams (1957), Villiers (1958), Marquez (1970) and Hughes (1974).

1.2.2 Taxonomic status

The hawksbill turtle is a morpho-species.

1.2.3 Subspecies

Agassiz (1857) described an Atlantic, E. imbricata, and a Pacific, E. squamata, hawksbill species based on differences in the arrangement of carapace keels and body shape. The young of both species were similar

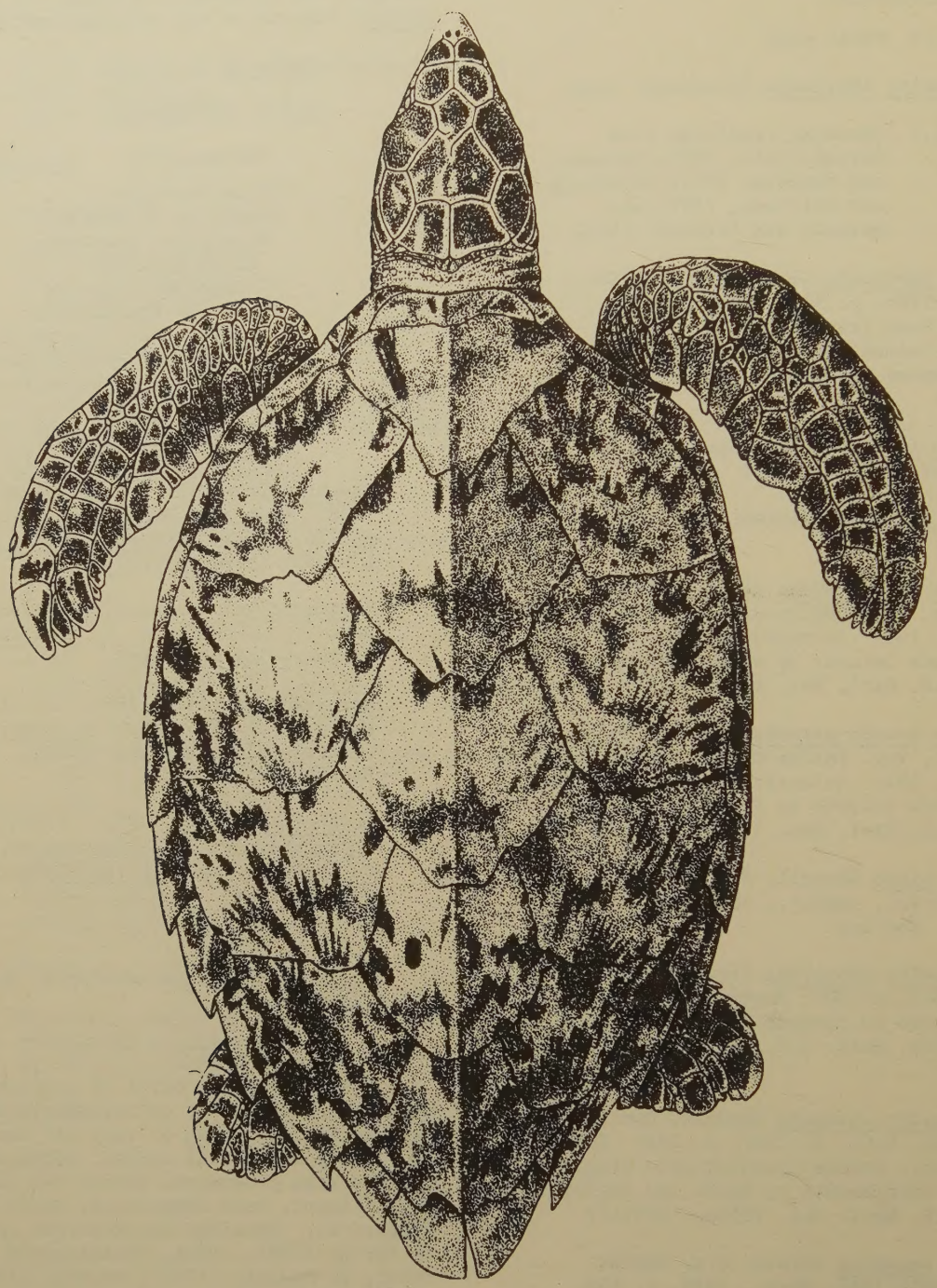

Figure 1 Juvenile hawksbill turtle (from Brongersma, 1968)

(heart-shaped), but the Atlantic species became more elliptical with age while the Pacific species remained heart-shaped. Deraniyagala (1939) could not distinguish separate Atlantic and Indo-Pacific species after examining illustrations, literature, and corresponding with various museums concerning carapace osteology. Schmidt (1945) was disappointed that sea turtle taxonomy was in such an unsatisfactory state due to the unwarranted tendency to separate Atlantic, Indo-Pacific and eastern Pacific species in each genus and concluded that an adequate comparison of hawksbill specimens of all size classes from all three regions was needed. Carr (1952) stated that the keel characters described by Agassiz (1857) were unreliable because they are subject to variation dependant upon individual age and sex. Carr (1952) then proposed a subspecific designation based on coloration and carapace shape. The Atlantic hawksbill, E. i. impricata (Linnaeus), is reportedly less black on the dorsal surface of the flippers and head, and the carapace is more straight-sided and narrowly tapered posteriorly. The Indo-Pacific subspecies, E. i. squamata Agassiz, is reportedly solid black on the dorsal surface of the flippers and head, and the carapace is more heart-shaped. In two publications, in Mexico, Secretaría de Industria y Comercio (1966) and in Marquez (1970), these characters are also used to describe Mexican Atlantic and Pacific hawksbill subspecies.

Variations in these characters cast doubt upon the validity of the subspecific designations. The carapace outline of Sri Lankan hawksbills changes with age from heart-shaped to more elongate (Deraniyagala, 1939), and Roze (1955) reported that Venezuelan hawksbills were basically heart-shaped, although shape varied with age. Hirth and Carr (1970) found no clear departure from colouration or body form between Gulf of Aden and Caribbean turtles, and Hughes (1974) reported western Indian Ocean and eastern Atlantic stocks mixed around the Cape of Good Hope, thereby providing further evidence against the subspecific taxonomic separation. Smith and Taylor (1950a), and more recently Hughes (1974), were unable to separate hawksbill subspecies based on colouration and morphology. Also, Loveridge and Williams (1957) deferred from identifying any subspecies and Frazier (1971) suggested that the subspecific designation be dropped. However, Pritchard (1979) stated that the eastern Pacific populations are darker and smaller than the Atlantic populations, and he believed that there are several undescribed subspecies of both in different parts of the world. The apparent variations in colour and morphology between nesting populations, and individuals of different age and sex within these populations, may account for the original subspecific designation (see section 1.3). Morphometric, electrophoretic and serologic studies are lacking for proper population comparisons.

1.2.4 Standard common names

Hawksbill turtle, tortoise shell turtle (English); tortue caret (French); tortuga de carey (Spanish); taimai (Japanese).

1.2.5 Definition of size categories

Size categories for hawksbill turtles are defined as follows:

(1) hatchling - freshly hatched turtle with umbilical scar, to 8 cm;

(2) juvenile - umbilical scar absent, 9-33 cm (approximately one-half carapace length of reproductively mature female);

(3) subadult - carapace length, 34-65 cm; and

(4) adult - reproductively mature, 66+ cm.

1.3 Morphology

1.3.1 External/internal morphology and colouration

General hawksbill morphology is described in Deraniyagala (1930, 1939, 1953); Carr (1952); Rebel (1974); Hughes (1974), and is illustrated in Stejneger (1904, 1907). See section 1.2.1.

The hawksbill turtle subspecific designations, which are discussed in section are based on colouration and carapace morphology. Consequently, the major references containing morphometric data, colour descriptions and photographs are given in this section, as well as the geographic locations and size classes of the turtles involved.

Morphometric measurements of hawksbills are presented in the following sources: Deraniyagala (1930, 1939, 1953), Sri Lanka, hatchlings, juveniles, subadults and adults; Carr, Hirth and Ogren (1966), Costa Rica, hatchlings, adult males and females; Pritchard (1966), Guyana, adult females; Hirth and Carr (1970), South Yemen, adult females; Frazier (1971), Aldabra, subadults; Japanese Tortoise Shell Association (1973), Japan (Singapore?) and Malaysia, juveniles and subadults (with some morphometric analysis); Hughes (1974), South Africa, juveniles and subadults (with morphometric analysis and length:weight relationship); McKeown (1977), Solomon Islands, adult females; McElroy and Alexander (1979), Solomon Islands, juveniles, subadults, adults (length:weight relationships only); Uchida (1979, 1980), Indonesia, juveniles, subadults and adults (length:weight relationship and some morphometric analysis). See section 3.4.3.

The hawksbill's carapace undergoes unique morphological changes with age, as described by Deraniyagala (1939): the carapace is cordate in outline with juxtaposed scutes in very young turtles, beginning to imbricate

when about 5 cm long (carapace length); scutes fully imbricated at about 15 cm and the marginals strongly serrate at 28.5 cm; scutes juxtaposed and carapace more elongate, subovate in outline, marginals less serrate at about 74 cm.

An account of Samoan hatchling, juvenile and adult colouration is as follows (Witzell and Banner, 1980): neonate colouration is uniform, variations are generally noticed when the turtles are about five months old; the carapace and the top of the head and neck are tan; the sides and bottom of the head and neck, including the beak, are dark grey; the dorsal and ventral sides of the fore flippers are grey with a whitish fringe around the posterior edge; the dorsal and ventral sides of the hind flippers and plastron are dark grey with two whitish ridges posteriorly on the plastron. Juvenile colouration is often variable, particularly the carapace, which ranges from light brown to black with varying amounts of distinct yellow streaks and blotches; the head and dorsal flipper scalation is black with whitish margins and the plastron is whitish with many brown blotches; the ventral side of the flippers has scattered black scales. The carapace in adult turtles is dark brown with faint yellow streaks and blotches; the scales on the dorsal side of the flippers and head are dark brown to black with yellow margins; the ventral side of the flippers and the plastron are pale yellow, with scattered dark scales on the flippers.

Colour descriptions of hawksbills are presented in the following sources: Deraniyagala (1930, 1939), Sri Lanka, hatchlings, juveniles, subadults and adult females; Carr (1952), Atlantic, hatchlings and turtles of unknown age, Pacific coast of Honduras, young and adult females; Villiers (1958), Senegal, juveniles and adults; Minton (1966), Pakistan, juveniles; Hirth and Carr (1970), South Yemen, hatchlings and adult females; Hughes (1974), South Africa, juveniles, subadults and adults; McKeown (1977), Solomon Islands, adults; Hirth and Latif (1980) Sudan, adult females; Vaughan (1981), Solomon Islands, hatchlings, juveniles and adults.

Hawksbill turtle colouration is apparently highly variable and may be due to either genetic or environmental factors. Adult hawksbills in the Solomon Islands become blacker with age according to McKeown (1977), and Frazier (1971) reported that the dorsal scalation of the juveniles, subadults and adults observed at Aldabra was black. Juvenile colouration is highly variable in South Africa (Hughes, 1974) and Samoa (Witzell and Banner, 1980). Carapace colouration of hawksbills on individual Torres Straits Islands was found to be homogeneous in pigmentation and pattern but differed markedly from island to island (Carr and Main, 1973; Bustard, 1979). Hirth and Carr (1970) reported that there was no special colour trend in eastern Pacific hawksbills (there being no clear departure in colouration from the Caribbean populations), and the colouration of nesting populations in the Gulf of Aden and Solomon Islands was also found to be variable (Hirth and Latif, 1980; Vaughan, 1981). Fryer (1911) reported that hawksbills remaining in Aldabra lagoon were always coated with a layer of mud which prevented the shell from developing dark markings, and Hornell (1927) and Stoddart and Wright (1967) also believed that there was a resident light-coloured population in Aldabra and Cosmoledo lagoons.

Photographs illustrating general morphology and colour patterns of hawksbill turtles are presented in the following sources: Schmidt (1916), Virgin Islands, dorsal of hatchlings; Taylor (1921), the Philippines, dorsal, ventral, anterodorsal and posteroventral of juveniles; Deraniyagala (1939, 1953), Sri Lanka, dorsal and ventral of juveniles, dorsal and anterodorsal of adult females; Carr (1952), Pacific Honduras, dorsolateral and lateral of adult females, ventral of juveniles; Villiers (1958, 1962), West Africa, dorsolateral and lateral of head of subadults, and (1958) dorsal and ventral of juveniles; Carr, Hirth and Ogren (1966), Costa Rica, dorsal of hatchlings, dorsolateral of juveniles, ventral, anterior and posterior of adult females; Taylor (1970), the Philippines, anterodorsal, posteroventral and dorsal of juveniles; Hughes (1971), Mozambique, dorsal of juveniles; Bustard (1972), Australia, dorsolateral and dorsoanterior of juveniles; Janssen (1972), Suriname, anterior and lateral of adult females; Carr and Main (1973), Australia, dorsal of juveniles; Hughes (1974), South Africa, dorsal of carapace and lateral of head; Heang (1975), Malaysia, dorsolateral of juveniles and anterodorsal of adult females; Schulz (1975), Suriname, dorsolateral and anterodorsal of head of adult females; Hughes (1976), Mauritius, dorsal of juveniles; Pritchard (1977), Micronesia, ventral of juveniles; Pritchard (1979), eastern Pacific, anterodorsal of juveniles; Pritchard (1979a), Grand Cayman, dorsolateral of juveniles, and Galapagos, ventral and lateral of head; Witzell and Banner (1980), Samoa, dorsal of hatchlings, dorsolateral of juveniles, dorsal and ventral of adult males, dorsal and lateral of head of adult males.

Anatomical studies of the hawksbill are not only incomplete, but are often confusing because of changes in terminology. Also, many of the publications have been overlooked over the decades because they have been difficult to locate and translate into English. The first attempt at general anatomy was made by Hoffmann (1890), who described the systematics and general anatomy of turtles, with some particular comments on the hawksbill. He illustrated the bones of the skull, flipper and hyoid apparatus, as well as the neck and posterior musculature, urogenital area, nose, upper eye, and histological sections of ribs, costal plate, plastron and spine.

Aspects of hawksbill skeletal anatomy are described and illustrated in numerous publications. Bellairs (1970) illustrated the hawksbill bony skeleton (Figure 2) and briefly discussed some general chelonian skeletal characteristics. Hoffstetter and Gasc (1969) described and illustrated hawksbill vertebrae and provided an extensive review of chelonian vertebral literature. The structure of the hyoid apparatus is described by Siebenrock (1899) and Fürbringer (1922), and is reviewed by Schumacher (1973). In a series of articles, Fuchs (1920, a, b, c) described the ossification of the cranial endoskeleton in sea turtles, with appropriate comments on the hawksbill. Skull structure is described and illustrated in detail by Feuer (1970) and illustrated by Temminck and Schlegel (1838), Boulenger (1889, 1890), Deraniyagala (1939) and Carr (1952), and photographed dorsally and ventrally by Villiers (1958). Carapace and plastron ossification (Figure 3) are described and illustrated by Deraniyagala (1939, 1953), Mlynarski (1961) and Bellairs (1970a). In addition, there are several papers dealing with fossil chelonians which present some aspects of hawksbill skeletal anatomy while discussing phylogenetic relationships. Zangerl (1953, 1958, 1980) studied the morphology and phylogeny of Oligocene and recent sea turtles and provides an extensive review of the subject, including detailed osteological descriptions and illustrations of the following selected hawksbill anatomical features: fore limb, hind limb, skull, carapace, plastron, humerus, and an X-ray of an entire juvenile specimen. Zangerl and Turnbull (1955) discussed the significance of the morphology of the Miocene sea turtle, Procolpochelys grandaeva (Leidy) and the related Oligocene sea turtle, Euclastes melii, in determining the phylogeny of the modern sea turtle genera, also presenting various aspects of hawksbill skeletal anatomy. Mlynarski (1959) found some anatomical similarities between the Oligocene cheloniid Glarichelys knorri (Gray) and modern hawksbills, specifically the suprapygale and the hypoplastron.

Aspects of hawksbill turtle musculature and associated nerve innervations are described and illustrated in numerous publications. Sieglbauer (1909) described the musculature and innervation of the limbs, and Kriegler (1961) described and illustrated the pelvic limb musculature and innervations. The hawksbill pectoral limb musculature is described and illustrated by Shah and Patel (1964), and Walker (1973) provided an extensive review and discussion of the locomotor apparatus, illustrating the osteological structure of the rear foot. George and Shah (1959, a) and Shah (1962) described and illustrated the respiratory mechanism in hawksbills, and suggested that differences in this mechanism between terrestrial, semi-aquatic and aquatic species (hawksbills) illustrate possible evolutionary lines through adaptive radiation. Hawksbill inspiration is controlled by the contraction of the Serratus magnus anteriorly and the Obliquus abdominis posteriorly, and expiration by the joint action of the Transversus abdominis posteriorly and the Diaphragmaticus anteriorly (George and Shah, 1959, a, 1962). Certain back and abdominal muscles are illustrated by Rathke (1848). Hawksbill jaw musculature and innervation have been studied and illustrated by Lakjer (1926) and studied by Poglayen-Neuwall (1953) and Schumacher (1956, a). Also, Schumacher (1973) described in detail the jaw and laryngeal musculature with the associated innervations and provided an extensive review of previous studies. Further studies on hawksbill cranial nerves are by Fuse (1920), Fuchs (1933) and Soliman (1964), who described and illustrated the cranial nerves in detail and provided a literature review on the subject.

The internal relief of the hawksbill turtle digestive tract was described by Jacobshagen (1920), described and illustrated by Pernkopf and Lehner (1937), and is redescribed and reviewed by Parsons and Camaron (1977). They described the esophagus as being lined with long, conical, cornified papillae which project posteriorly and the duodenum as a complex network of transverse and longitudinal folds. The histology of the stomach musculature is described by Luppa (1977); the tunica muscularis is smooth muscle consisting of two layers, the inner one being circular and the outer one longitudinal, the thickness decreasing in the direction of the pyloris. According to Smith and James (1958), cloacal bursae, which function as respiratory organs during hibernation in some tetrapods, are absent in hawksbills.

The nasal cavities of hawksbill turtles have been described and illustrated by Fuchs (1907, 1911, 1915). In a series of exhaustive articles on the chelonian nasal cavity and associated glands, Parsons (1958, 1959, 1968, 1970) described and illustrated the generally single choanal papilla as varying in shape, but usually as a stiff thorn-like structure projecting medially into the choana. Parsons discussed its possible function as either a special sensory organ or to prevent food from entering the nasal cavities. Based on nasal morphology, specifically the increasing complexity of the regio intermedialis and the comparative reduction of the regio olfactoria, Parsons arranged the following sea turtle genera in order of increasing adaptation to the aquatic environment: Celonia, Caretta, Eretmochelys and Dermochelys. See section 3.2.1.

Underwood (1970) described and reviewed previous studies on the reptilian eye, and reported (with illustrations) that hawskbills have 12 scleral ossicles in a scleral ring, which has a denticulate periphery with irregular overlapping borders and a ciliary body with 66 ciliary processes.

The urogenital apparatus and associated organs of a female hawksbill turtle have been

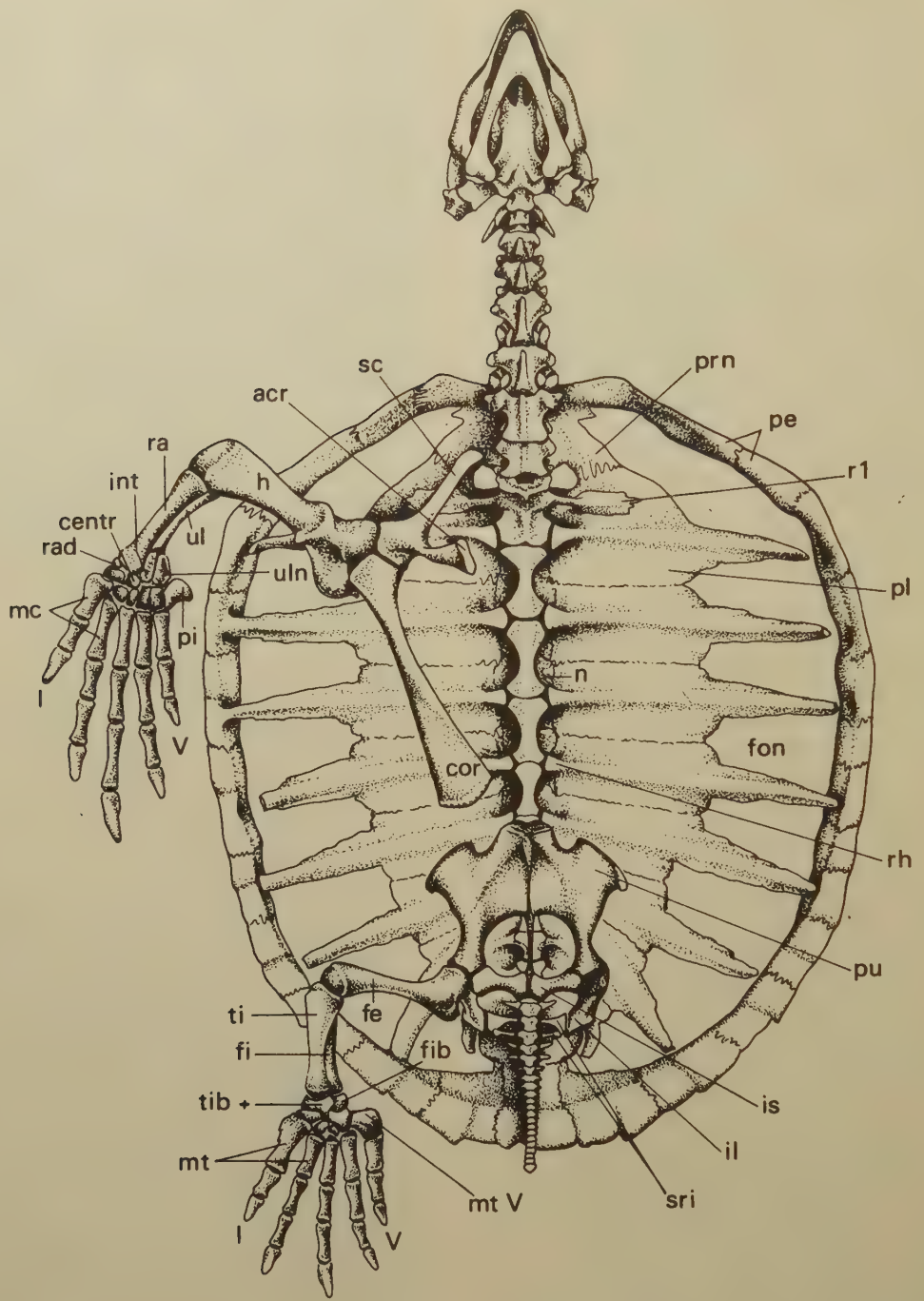

Figure 2 Bony skeleton of the hawksbill turtle:
acr - acromion process of scapula; centr - centrale; cor - coracoid; fe - femur; fi - fibula; fib - fibulare (calcaneum); fon - fontanelle in bony carapace; h - humerus; il - ilium; int - intermedium; is - ischium; mc - metacarpals; mt - metatarsals; n - neural bony plates; pe - peripheral plates; pi - pisiform; pl - pleural plates; prn - proneural (nuchal) plate; pu - pubis; ra - radius; rad - radiale; rh - rib head; r1 - first dorsal rib; sc - scapula; sri - sacral ribs; ti - tibia; tib+ - tibiale fused with other elements (astragalus); ul - ulna; uln - ulnare; I, V - digits (from Bellairs, 1970)

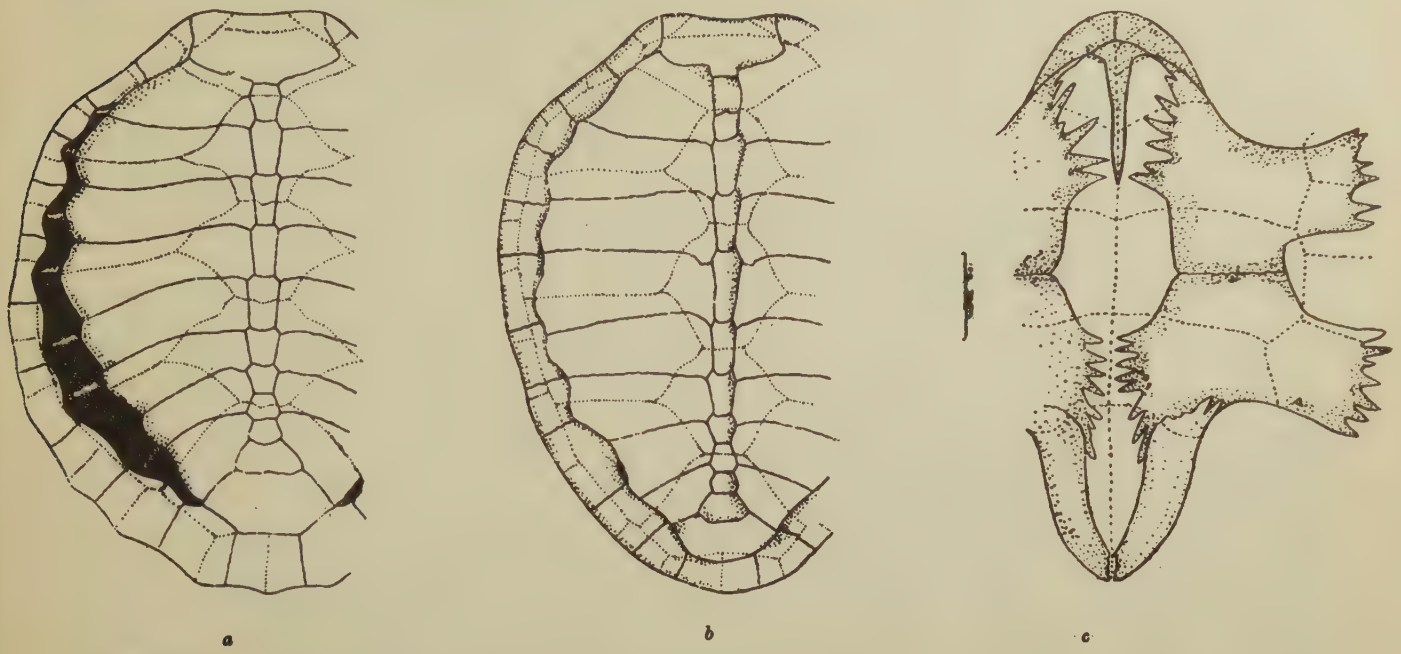

Figure 3 Carapace and plastron ossification of the hawksbill turtle: (a) carapace of subadult; (b) carapace of mature female (X 1/6); (c) plastron of mature female (X 1/6); black = vacuities (from Deraniyagala, 1953)

described and illustrated by Schmidtgen (1907). Zug (1966) reviewed penial morphology and the systematic relationships of cryptodiran turtles, concluding that all genera of Cheloniidae are similar in structure: a single U-shaped fold forms the glands, this fold appearing to be an enlarged continuation of the seminal ridge, with a single seminal groove that terminates on the inner surface of the fold, and no observed sinuses; the genitalia of an immature hawksbill is illustrated.

Sapsford (1978) examined the hawksbill pulmonary artery, finding the presence of a sphincter muscle distal to the origin of the Ductus botalli, and postulated that right to left intra-cardiac blood shunts occur during diving which may aid in thermal regulation.

Walker (1971) illustrated and described the anatomy and swimming dynamics of hawksbills and found them to be similar to other sea turtles. They swim by moving the blade of the pectoral flipper up and down along a line inclined from 40° to 70° from the horizontal plane. The leading edge of the blade is inclined anteroventrally on the downstroke and anterodorsally on the upstroke, and the blade tip usually inscribes a figure 8. The downstroke is the main propulsive stroke, but some propulsive components are generated on the upstroke. The rear flippers extend posteriorly beyond the edge of the shell, close to the horizontal plane and act as rudders and elevators.

1.3.2 Cytomorphology

Dujarric de la Riviere, Fine and Eyquem (1954) studied the hetero-agglutination of hawksbill turtle sera combined with sera of Chelonia mydas and several species of domestic mammals. Frair (1977) reported that the following Atlantic hawsbill red blood cell parameters are correlated with the increase of carapace length; increase in packed cell volume, decrease in red cell counts and an increase in red cell size and volume. Frair (1977a) also reported red blood cell packed volumes, sizes and numbers (Table I).

Table I

Red blood cell parameters of Atlantic hawksbill turtles (modified from Frair, 1977a)

	Packed cell volume (cm^3/100 cm^3)	Length/Width (μm)	Red cell count (/mm^3 x 10^3)
Mean	28.1 ± 1.2	22.6 ± 0.3/14.8 ± 0.3	421 ± 41
Range	17-42	16.5-28.0/9.6-19.5	366-478
Sample	25	13	6

Owens and Ruiz (1980) described new methods of obtaining blood and cerebrospinal fluid from hawksbills via the paired dorsal cervical sinuses and through the foramen magnum into the brain's fourth ventrical without causing stress or damage to the animals.

The hawksbill karyotype is 56 chromosomes (Bickham, 1979) which are nearly identical to those of Chelonia mydas and Caretta caretta; no sex chromosomes were identified.

1.3.3 Protein composition and specificity

The serum protein concentration of an immature Atlantic hawksbill turtle was 1.9% (Frair, 1964). Further serological studies by Frair (1969) suggested the hawksbills' close affinity with the other sea turtle genera, and found that sera stored as sterile liquid lost about a third of their reactivity after ten years of cold storage. Continued serological tests by Frair (1979, a) showed a close affinity between hawksbill, Caretta, and Lepidochelys turtles. Chen, Mao and Ling (1980), in another study of the evolutionary relationships of turtles, calculated the immunological distances among albumins and estimated that the divergence time for the hawksbill genus to be 29 million years.

Lysine/histidine ratio analysis of Atlantic hawksbill and Chelonia mydas carapace scute material showed a significant genetic difference between these genera (Hendrickson, Wood and Young, 1977). After further analysis, Hendrickson (1979) found no particular strong variations in amino acid ratios between west Atlantic, west Pacific and Indian Oceans hawksbills. Although some variations were probably caused by diet, Hendrickson concluded that there was either within-group heterogeneity or that there were no significant differences between local populations.

The carapace scutes of "tortoise-shell" fame are composed of keratin, the physical properties of which were discussed by Smith (1958), Hoepli (1965) and Webster (1972); refractive index is 1.55, specific gravity is 1.29 and hardness is 2.5 on Moh's scale. Baden and Maderson (1970) used standard histological and X-ray diffraction techniques to examine the types of fibrous protein layers produced by ammiote epidermal cells and found that the hawksbill shell showed a feather-type pattern, while scales from the rest of the body showed a feather-type on the outer surface and an alpha-type in the hinge region; an arrangement resulting in a more pliable tissue and hence greater skin flexibility. The X-ray diffraction pattern showed a distinct 4.15 $\AA$ reflection oriented on the meridian in the alpha-layer.

Body fat composition of a wild Indian Ocean hawksbill turtle was found by Pathak and Dey (1956) to have significant differences when compared to turtle fat from other species. A high unsaturated acid content is reportedly typical of marine species, but the hawksbill's decrease in unsaturated C_{18} acid content and increase in amounts of higher unsaturated acids of C_{20}, C_{22} and C_{24} were found to be different from other turtles and were attributed to species differences, diet differences, or both, between wild and captive specimens.

An analysis of hawksbill turtle eggs in Indonesia showed the following percentages: protein, 22.02%; fat, 16.43%; fibre, 0%; ash, 3.03%; and water, 59.34% (Suwelo, 1971).

2. DISTRIBUTION

2.1 Total Area

Hawksbill turtles are circumtropical, generally inhabiting coastal reefs, bays, estuaries and lagoons in the tropical and subtropical Atlantic, Pacific and Indian Oceans. The hawksbill is perhaps the most tropical of all marine turtles. The major nesting and foraging areas are located between the Tropics of Cancer and Capricorn, with the exception of the Persian Gulf populations, although turtles are occasionally seen out to 30° latitude, with strays extending into colder waters. Specific nesting locations are discussed in section 3.1, listed in Table II, and delineated in Figure 4. Non-nesting range extensions are many, and a brief summary by ocean follows.

Distributional information on hawksbills in the eastern and mid-Atlantic Ocean is scarce. Brongersma (1967, 1972) confirmed a stray hawksbill from the European coast of the English Channel, and Loveridge and Williams (1957) have recorded hawksbills from the following localities in Africa: Mauritania, Senegal, Sierra Leone, Liberia, Ghana, Cameroon, Gabon and South Africa. Hawksbills have also been recorded from: Morocco (Bons, 1972); Mauritania (Maigret, 1975); Senegal (Cadenat, 1949, 1957; Villiers, 1958, 1962; Maigret, 1975, 1977, 1978); Gambia (Brongersma, 1981); Ghana (Irvine, 1947; Anon., 1971); Togo (Villiers, 1958); Cameroon (Nieden, 1910; Brongersma, 1981); Angola (Hughes, Huntley and Wearne, 1973); South Africa (Hughes, 1974). Island localities include Madeira (Maul, 1948; Brongersma, 1968), Cape Verde Islands (Loveridge and Williams, 1957; Schleich, 1979), Ascension Island (Loveridge and Williams, 1957; Carr and Stancyk, 1975; Mortimer, 1981), and Saint Helena (Brongersma, 1971). Hawksbills are collected at sea from the "H.M.S. CHALLENGER" 350 mi west of the Azores Islands, 25 mi west of Cape Saint Vincent, Portugal and half way between Cape Saint Vincent and Madeira (Murray, 1895). A definitive work on hawksbill distribution in the eastern Atlantic Ocean is by Brongersma (1981).

Table II

Nesting locations and nesting seasons of hawksbill turtles
(parentheses indicate reported major nesting months)

Nesting location	Nesting season J	F	M	A	M	J	J	A	S	O	N	D	Sources
Eastern Atlantic Ocean													
Gulf of Guinea	X	X									X	X	Greef (1885); Loveridge and Williams (1957); Eisentraut (1964)
Liberia													Buttikofer (1884, 1890); Brongersma (1981)
Western Atlantic Ocean													
United States Florida				X	X	X	X	X					Garman (1883, 1884); True (1893); Audubon (1926); De Sola (1935); Carr, Hirth and Ogren (1966); Lund (1978)
Mexico				X	X	X	X	X	X	X			Carr (1952); México, Secretaría de Industria y Comercio (1966); Ramos (1974); Marquez (1976, a, 1978); Caribbean Conservation Corporation (1980); Hildebrand (1981); Bacon (1981)
Belize													Bacon (1975, 1981); Caribbean Conservation Corporation (1980)
Guatemala													Bacon (1975, 1981); Caribbean Conservation Corporation (1980)
Honduras													Caribbean Conservation Corporation (1980); Bacon (1981)
Nicaragua						X	(X	X)	X	X			Nietschmann (1971, 1972, a, b); Rainey and Pritchard (1972); Bacon (1975, 1981); Carr and Stancyk (1975); Caribbean Conservation Corporation (1980)
Costa Rica					(X	X)	X	X	X	X			Carr, Hirth and Ogren (1966); Bacon (1975, 1981); Carr and Stancyk (1975); Carr, Carr and Meylan (1978)
Panama				X	(X	X)	X	X					Carr (1956); Duke (1967); Rainey and Pritchard (1972); Tovar (1973); Bacon (1975, 1981); Carr and Stancyk (1975); Caribbean Conservation Corporation (1980)
Colombia				X	X	X	X	X	X	X			Parsons (1956); Medem (1962); Kaufmann (1966, 1967, 1971, 1972, 1975); Rainey and Pritchard (1972); Tufts (1973); Bacon (1975); Bullis (1978); Caribbean Conservation Corporation (1980)

Table II (continued)

Nesting location	Nesting season J	F	M	A	M	J	J	A	S	O	N	D	Sources
W. Atlantic Ocean (continued)													
Venezuela					X	X	X	X					Larrea (1948); Roze (1955, 1964); Donoso-Barros (1964); Flores (1969); Caldwell and Rathjen (1969); Bacon (1975, 1981); Buitrago (1980); Caribbean Conservation Corporation (1980)
Guyana			X	X	X	X	X	X					Pritchard (1966, 1969a, b); Bacon (1975, 1981); Schulz (1975)
Suriname		X	X	X	(X	X	X)	X					Schulz (1969, 1971, a, 1975, 1981); Brongersma (1968a); Pritchard (1969a); Bacon (1975, 1981)
French Guyana					X	X							Pritchard (1969, 1971); Schulz (1971); Bacon (1975, 1981); Fretey (1976); Fretey and Lescure (1976, 1979)
The Bahamas	X	X	X	X	X	X	X	X	X	X	X	X	Nye (1887); Caribbean Conservation Corporation (1980); Bacon (1981)
Turks and Caicos Islands													Caribbean Conservation Corporation (1980); Bacon (1981)
Cuba													Martinez (1948); Ubeda (1973); Bacon (1975); Carr and Stancyk (1975)
Cayman Islands													Lewis (1940); Bacon (1975, 1981)
Jamaica				X	X	X	X	X			X		Thompson (1945); Caldwell (1961); Bacon (1975, 1981); Carr and Stancyk (1975); Caribbean Conservation Corporation (1980)
Dominican Republic													Ross (1980); Caribbean Conservation Corporation (1980)
Puerto Rico	X				X	X	X	X	(X)	X	X	X	Wilcox (1904); Schmidt (1916); Bacon (1975, 1981); Carr and Stancyk (1975); Thurston (1976); Thurston and Wiewandt (1976); Carr (1977, 1978); U.S. Fish and Wildlife Service (1978); Dodd (1978)
Virgin Islands						X	X	X	X	X	X		Schmidt (1916); Bacon (1975, 1981); Philibosian (1976); Dodd (1978); Towle (1978); Caribbean Conservation Corporation (1980)
Barbuda													Cato, Prochaska and Pritchard (1978)

Table II (continued)

Nesting location	Nesting season J	F	M	A	M	J	J	A	S	O	N	D	Sources
W. Atlantic Ocean (continued)													
Antigua													Cato, Prochaska and Pritchard (1978)
Montserrat													Bacon (1975)
Guadeloupe				X	X	X	X	X	X				Kermarrec (1976); Caribbean Conservation Corporation (1980); Bacon (1981)
Dominica													Bacon (1975, 1981)
Martinique		X	X	X	X	X	X	X	X				Kermarrec (1976); Caribbean Conservation Corporation (1980); Bacon (1981)
Saint Lucia				X	X	X	X	X	X	X			Cato, Prochaska and Pritchard (1978); Caribbean Conservation Corporation (1980); Bacon (1981)
Saint Vincent			X	X	X	X	X	X	X				Caribbean Conservation Corporation (1980); Bacon (1981)
Grenadines				X	X	X	X	X	X				Carr and Stancyk (1975); Caribbean Conservation Corporation (1980); Bacon (1981)
Grenada				X	X	X	X	X	X	X			Carr (1952); Bacon (1975, 1981); Caribbean Conservation Corporation (1980); Goodwin (1980, 1981)
Trinidad and Tobago				X	X	X	X	X	X				Carr (1954); Bacon (1971, 1975, 1981)
Eastern Pacific Ocean													
Mexico					X	X	X	X	X	X	X		Stejneger (1899); Marquez (1970); Casas (1971)
El Salvador							X	X	X	X	X	X	Cornelius (1981)
Honduras								X	X	X	X		Carr (1952); Cornelius (1981)
Nicaragua													Nietschmann (1975); Cornelius (1981)
Costa Rica													Cornelius (1981)
Panama					X	X	X	X	X	X	X	X	Cornelius (1981)
Ecuador (Mainland)	X	(X)	X	X	X							X	Green and Ortiz-Crespo (1981)

Table II (continued)

Nesting location	Nesting season J	F	M	A	M	J	J	A	S	O	N	D	Sources
E. Pacific Ocean (continued)													
Ecuador (Galapagos Is.)													Pritchard (1971a)
Easter Island													Pritchard (1981)
Central Pacific Ocean													
United States Hawaii													Sakuda (1969); Balazs (1978, 1981); Shomura (1979)
Trust Territories of the Pacific Islands (Micronesia)	X	X	X	X	(X	X	X	X	X)	X	X	X	Nakajima (1920); Fukada (1965); Trust Territories of the Pacific Islands (1957); Helfman (1968); Hendrickson (1972); McVey (1972); Marshall (1975); Pritchard (1977, 1978, 1981a); Dodd (1978); Shomura (1979); McCoy (1981)
Line Islands													Balazs (1978); Shomura (1979)
Tokelau Islands									X	X			Hirth (1971, a); Balazs (1978, 1981)
Western Samoa	(X	X)							X	X	X	X	Witzell (1972, 1974); Witzell and Banner (1980)
American Samoa							X	X	X				Graeffe (1873); Sachet (1954); Hirth (1971, a); Dodd (1978); Balazs (1981)
Fiji	X	X									X	X	Bustard (1970); Raj (1976); Pritchard (1981)
Kingdom of Tonga	(X	X)								X	X	X	Hirth (1971, a); Wilkinson (1979); Pritchard (1981)
Cook Islands													Balazs (1981)
French Polynesia													South Pacific Commission (1979)
Solomon Islands	X)	X	X	X	(X	X	X	X)	X	(X	X	X	McKeown (1977); McElroy and Alexander (1979); Pritchard (1981); Vaughan (1981)
New Hebrides	X								X	X	X	X	South Pacific Commission (1979); McElroy and Alexander (1979); Pritchard (1981)
Western Pacific Ocean													
China			X	X									Chu-Chien (1981)
Democratic Kampuchea	X	X										X	Le Poulain (1941)

Table II (continued)

Nesting location	Nesting season J	F	M	A	M	J	J	A	S	O	N	D	Sources
W. Pacific Ocean (continued)													
Thailand	X)	X	X	X	(X	X	X	X)	X	X	X	(X	Penyapol (1958)
Malaysia	(X	X	X	X	X)	X	(X	X	X	X)	X	X	Banks (1937); Hendrickson and Alfred (1961); Harrisson (1964, 1969); Hendrickson and Balasingam (1966); Balasingam (1969); De Silva (1968, 1969, a, b, 1971, 1981); Heang (1975); Uchida (1979, 1980); Tow and Moll (1981)
Indonesia	X	X	X	X)	X	X	X	X	X	(X	X	X	Suwello (1971); Japanese Tortoise Shell Association (1973); Kajihara and Uchida (1974); Sumertha (1976, 1979, 1980); Sumertha and Sukarma (1977); MacKinnon (1979); Uchida (1979, 1980); Polunin and Sumertha (1981)
Japan Ryukyu Islands				X*	X	(X	X)						Hendrickson (1965); Robles (1975); Uchida and Nishiwaki (1981)
Philippines	X	X	X	X	X	X	X	X	X	X	X	X	Seale (1911); Domantay (1952-53); Japanese Tortoise Shell Association (1973); Negeri and Tow (1977); Alcala (1980); De Celis (1981)
Papua New Guinea	X		X	X	X	X	X	X	X			X	Papua New Guinea, Ministry of Environment and Conservation (1978); Spring (1981)
Australia	X	X	X	X	X	X	X	X	X	X	X	X	Bustard (1971, 1972, a, 1973); Carr and Main (1973); Limpus (1978, 1980, 1981); Kowarsky and Capelle (1979)
Indian Ocean													
India	X	X	X	X	X	(X	X	X	X	X)	X	X	Raj (1927); Whitaker (1977); Bhaskar (1978, 1979); Kar and Bhaskar (1981)
Burma						X	X	X	X				Kar and Bhaskar (1981)
Iran				X	X	X							Walczak and Kinunen (1971); Anderson (1979); Ross and Barwani (1981)
Saudi Arabia (Persian Gulf)				X	X	X	X						Ross and Barwani (1981)

Table II (continued)

Nesting location	Nesting season J	F	M	A	M	J	J	A	S	O	N	D	Sources
Indian Ocean (continued)													
Qatar					X	X	X						Ross and Barwani (1981)
Oman	X	X	(X)	X	X								Ross (1981); Ross and Barwani (1981)
Yemen	X	X										X	Hirth and Carr (1970); Ross and Barwani (1981)
Sudan			X			X	X						Moore and Balzarotti (1976); Anon. (1977); Hirth and Latif (1980); Ross and Barwani (1981)
Yemen	X	X										X	Hirth and Carr (1970); Ross and Barwani (1981)
Ethiopia		X	X										Ruppell (1835)
Somalia													Frazier (1975)
Kenya													Frazier (1975, 1981)
Tanzania													Frazier (1975, 1976, 1981)
Mozambique													Hughes (1971, 1974)
Sri Lanka	X)	X		X	X	X					X	(X	Deraniyagala (1939, 1953); Carr (1952)
Maldives													Colton (1977); Shakeeb (1980)
Malagasy Republic													Hughes (1973, 1974, 1981); Frazier (1975, a)
Oceanic Island Groups (Chagos, Cocos, Comores, Seychelles)	X)	X	X	X	X		X	X	(X	X	X	X	Hornell (1927); Gibson-Hill (1950); Stoddard and Wright (1967); Frazier (1971, 1974, 1975, a, 1976, a, 1979, a, 1981); Hughes (1974); Diamond (1976); Salm (1976); Garnett (1978); Sheppard (1979); Garnett and Frazier (1979)

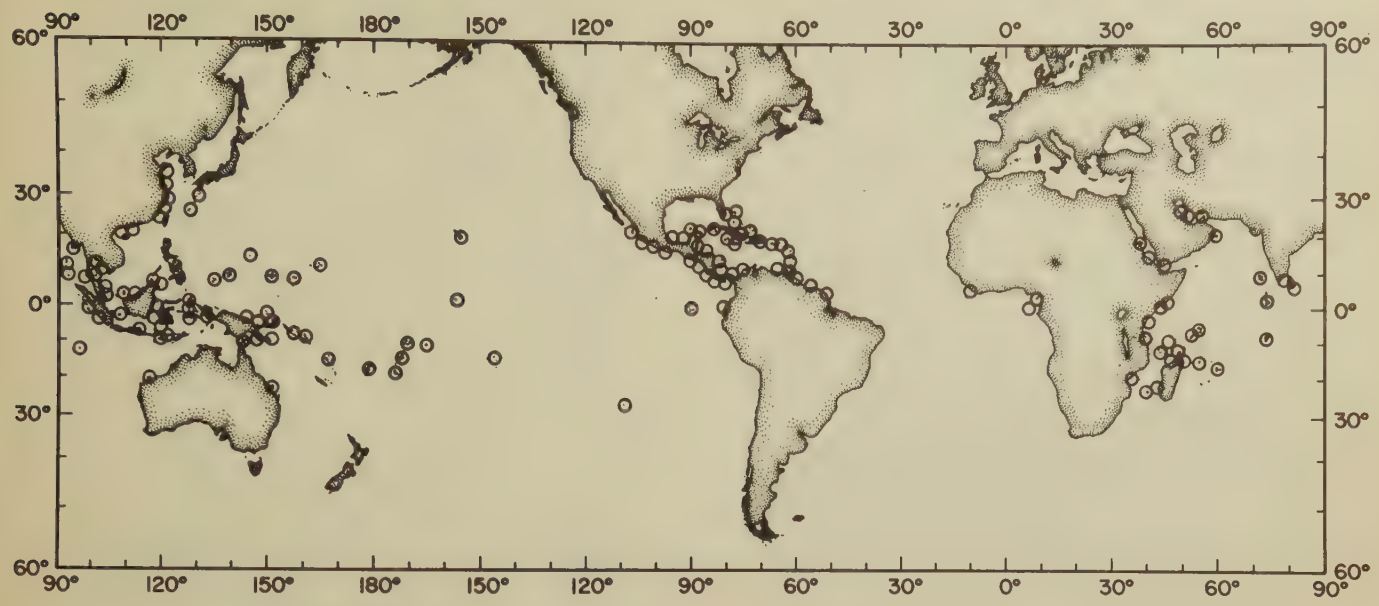

Figure 4 Documented nesting locations of the hawksbill turtle

Mediterranean records of hawksbill turtles are scarce, ranging from France (Mourgue, 1909; Angel, 1946) to the eastern coast (Gruvel, 1931; Sella, 1981; Wermuth and Mertens, 1961).

In the western Atlantic Ocean, hawksbills have been recorded as strays from Cape Cod, Massachusetts (Sumner, 1909; Sumner, Osburn and Cole, 1911; Bleakney, 1965; Lazell, 1980) and from Virginia (Musick, 1979). Hawksbills are occasionally found in North Carolina (True, 1887; Schwartz, 1961, 1976), but are rarely encountered in Georgia waters (De Sola and Abrams, 1933; Hillestad, Richardson and Williamson, 1978) and Bermuda (Garman, 1884). Hawksbills were once reported to nest frequently in Florida (Garman, 1883, 1884; True, 1893; Audubon, 1926; De Sola, 1935), but are now only very rare nesters, although they are still occasionally seen (Caribbean Conservation Corporation, 1980). However, they are uncommon in the northern Gulf of Mexico (Smith, 1954; Neck, 1978; Hildebrand, 1981). Hawksbills are common throughout the southern Gulf of Mexico, Caribbean Sea, northern South America, and reports are reviewed by Bacon (1975, 1981) and Caribbean Conservation Corporation (1980). Although once reported to nest infrequently in French Guyana (Pritchard, 1969, a, 1971), hawksbills have apparently stopped nesting and have become rare visitors (Fretey, 1976; Fretey and Lescure, 1976, 1979). The southern end of their range is northern Brazil (Goeldi, 1905; Luederwaldt, 1926; Froes, 1957; Menezes, 1972). In the Pacific Ocean, hawksbills have been reported in the eastern Pacific from the Gulf of California as far as 29° north (Caldwell, 1962; Aschman, 1966), throughout the northwestern states of Mexico (Duellman, 1961; Marquez, 1965; México, Secretaría de Industria y Comercio, 1966; Hardy and McDiarmid, 1969; Cliffton, Cornego and Felger, 1981), and south along the Central and South American coasts (Cornelius, 1981), to Colombia and Ecuador (Green and Ortiz-Crespo, 1981), Peru (Carr, 1952; Brown and Brown, 1981), and Chile (Yanez, 1951). Oceanic island records in the eastern Pacific list the hawksbills from the Revillagigedo Islands in the north (Marquez, 1965), the equatorial Galapagos Islands (Pritchard, 1971a, b; Honegger, 1972; Green and Ortiz-Crespo, 1981), and Easter Island in the south (Garman, 1908; Pritchard, 1981). The hawksbill is recorded in the northern central Pacific from the southern Hawaiian archipelago (Tinker, 1941; Oliver and Shaw, 1953; Balazs, 1977, 1978, 1981) and from the Sea of Japan in the west (Stejneger, 1907; Nishimura and Yasuda, 1967; Uchida and Nishiwaki, 1981), south along the China mainland (Gee, 1929-30; Pope, 1934, 1935; Chu-Chien, 1981) and Formosa (Swinhoe, 1863), through Indonesia (Japanese Tortoise Shell Association, 1973; Kajihara and Uchida, 1974; Uchida, 1979, 1980), to New Zealand (McCann, 1966) and Tasmania (Green, 1971). The hawksbill is also found throughout the many island groups of the central Pacific region (South Pacific Commission, 1979). Virtually all tropical Pacific island groups support populations of foraging hawksbills.

The hawksbill is reported in the northern Indian Ocean from Burma (Theobald, 1868), Pakistan (Minton, 1966; Khan and Mirza, 1976), the Persian Gulf (Khalaf, 1959; Anderson, 1979), the Red Sea (Flower, 1933; Anon., 1977; Hirth and Latif, 1980; Sella, 1981), and extending southerly to South Africa (Hughes, Bass and Mentis, 1967; Hughes, 1970, 1971a, 1974). The hawksbill is also found throughout the many oceanic island groups in the Indian Ocean (Frazier, 1974, 1975a, 1976a;

Hughes, 1974; Diamond, 1976). Major reviews of hawksbill distribution in the Indian Ocean are by Kar and Bhaskar (1981), Ross and Barwani (1981) and Frazier (1981).

2.2 Differential Distribution

2.2.1 Hatchlings

There is very little information regarding hatchling distribution, though it is suspected that they passively migrate with the prevailing oceanic currents (Carr, Hirth and Ogren, 1966). Hornell (1927) reported that a reliable witness had seen hatchling hawksbills drifting in masses of floating Sargassum weed miles from land. At least some hatchlings may remain on the reefs close to their natal beaches (Schmidt, 1916; Sumertha, 1976; Shomura, 1979; Uchida, 1979, 1980; Witzell and Banner, 1980).

2.2.2 Juveniles, subadults and adults

The distribution of hawksbills is generally centered around caroline reefs near the nesting beaches (Hornell, 1927; Hirth and Carr, 1970; Frazier, 1971; Japanese Tortoise Shell Association, 1973; McKeown, 1977; Caribbean Conservation Corporation, 1980; Witzell and Banner, 1980). These nesting areas, and the associated nesting seasons, are delineated in Figure 4 and summarized in Table II. Although the adults are generally seen in the proximity of the nesting areas year-round, they are often more abundant during the nesting season (Voeltzkow, 1897; Carr, Hirth and Ogren, 1966; Frazier, 1971; Bhaskar, 1978; Witzell and Banner, 1980).

Evidence suggests that some hawksbill turtles may be fairly sedentary, and others may migrate considerable distances. A resident hawksbill population existed in Aldabra lagoon, where local turtles could be distinguished by their unusual light colour, which was presumably due to a layer of mud covering the carapaces (Fryer, 1911; Hornell, 1927). Carr, Hirth and Ogren (1966) thought that the prevalence of barnacles on Costa Rican adults attested to a relatively sedentary life. However, they also presented circumstantial evidence of limited migratory travel, which is updated by Carr and Stancyk (1975). Carr (1977) provided evidence by sonic tagging that juveniles are fairly sedentary on Puerto Rican reefs. Tagging evidence in the Solomon Islands showed the hawksbill to be generally parochial, although some long distance movements were observed (McKeown, 1977; McElroy and Alexander, 1979; Vaughan, 1981). Kowarsky and Capelle (1979) reported tag returns of two pond-reared juvenile hawksbills from New Guinea. The turtles were released in the Torres Straits approximately 83 km and 70 km away, and were recaptured after being free for 151 and 204 days, respectively (see Table XIX). Garnett (1978), Frazier (in press) and Alcala (1980) concluded from limited tagging evidence that hawksbills tended to exhibit localized movements in the Seychelles and Philippines, respectively. See section 3.5.1

2.3 Determinants of Distributional Changes

Hawksbill distribution is centred around coral reefs, tropical water temperatures limit dispersal of hatchlings, juveniles, subadults and adults. Reproductive migrations of unknown distance from feeding areas to nesting beaches are suspected to occur at unknown intervals. See sections 2.1, 2.2, 3.1.6 and 3.5.1.

2.4 Hybridization

Turtle fishermen in the Cayman Islands, interviewed by Lewis (1940), said that a hybrid cross between Eretmochelys and Caretta, called a "McQueggie", was commonly seen in Central American waters. The fishermen were sure such a hybrid existed because they had often seen and captured Eretmochelys males which were copulating with Caretta females. However, Carr (1967) identified several "McQueggies" as recognizable turtle species and not as hybrids, stating that most of the folklore had no substance. Hendrickson (1980) reported seeing at the Cayman Turtle Farm what he considered were clearly the results of a hybrid cross between Chelonia mydas and E. imbricata. These turtles, hatched from a batch of wild eggs imported from Suriname, showed wide gradations and mixes of characters between the two species and is the first report of intergeneric mating involving hawksbills.

3. BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.1.1 Sexuality

Hawksbills are heterosexual with sexual dimorphism being evident in the adults. Adult males have a long, thick tail that extends well beyond the posterior margin of the carapace, long, heavy claws, and a soft, concave plastron. Also, Deraniyagala (1939) and Marquez (1970) reported that males have more intense pigmentation than females. Adult females have a short tail that does not extend appreciably beyond the hind margin of the carapace, shorter, thinner claws, and a harder, less concave plastron. Sexual distinction of hatchlings, juveniles and subadults is not possible by external examination, but only through dissection, histological examination, or radioimmunological tests.

3.1.2 Maturity

Carr (1952) reported that Caribbean hawksbills may be sexually mature at about three years of age when they are about 13.4 kg.

This weight estimate was revised by Carr, Hirth and Ogren (1966) to 35.7 kg with no corresponding age. Harrison (1963) felt that three turtles raised in Sarawak for 4 years appeared to be fully grown at a mean size and weight of 49.5 cm and 12.8 kg, respectively. The sizes of reproductively active turtles may be helpful when determining age to maturity, especially if hawksbills essentially stop growing after reaching maturity, as occurs in other marine turtle species (Carr and Goodman, 1970; Hughes, 1974). However, measurements and weights of mature turtles, particularly males, are scarce. Carapace length measurements of three adult Costa Rican males averaged 80.2 cm with a range of 79.3-81.3 cm (Carr, Hirth and Ogren, 1966). The mean and range sizes and weights of 17 adult male hawksbills from eastern Nicaragua are: 77.8 cm (71.4-85.0 cm); 53.4 kg (50.0-65.7 kg) (Nietschmann, 1972b). Sizes and weights of nesting hawksbills vary considerably and are presented in Tables III and IV, respectively.

Bustard (1979) reported age to maturity to be 3-4 years under favourable rearing conditions in Australia, and Witzell (1980) indicated that captive Samoan hawksbills may reach maturity at about 3.5-4.5 years of age.

Age and size at maturity are apparently quite variable between nesting populations; there are also differences between sexes and individuals within breeding populations (Witzell, 1980). These various size differences of different nesting populations are illustrated in Table III. See section 3.4.3.

3.1.3 Mating

Mating occurs on the surface in the shallow waters adjacent to the nesting beaches (Carr, 1954; Caldwell and Rathjen, 1969; Carr and Stancyk, 1975; Carr, Carr and Meylan, 1978). During copulation, the male uses the long heavy claws and tail, aided by the soft, concave plastron, to cling tightly to the

Table III

Carapace lengths of nesting hawksbill turtles[a/]

Location	Mean	Range	N	Source
Atlantic Ocean				
Nicaragua	76.5	62.5-87.0	32	Nietschmann (1972a)
Costa Rica	83.1	74.9-91.4	62	Carr, Hirth & Ogren (1966)
Colombia	90.7[b/]	88.0-95.0[b/]	4	Tufts (1973)
Guyana	83.8	80.0-88.9	23	Pritchard (1969)
Puerto Rico	77.6	67.1-85.6	4	Thurston & Wiewandt (1976)
Pacific Ocean				
Western Samoa	68.6	60.0-73.5	7	Witzell & Banner (1980)
Solomon Islands	80.5	68.0-93.0	85	McKeown (1977)
Solomon Islands	84.6[b/]	60.0-95.5[b/]	43	Vaughan (1981)
Australia	76.4	71.6-82.7	10	Limpus (1980)
Indian Ocean				
Seychelles	89.5[b/]	83.0-91.5[b/]	9	Diamond (1976)
Sudan	66.0	53.3-73.7	42	Hirth & Latif (1980)
South Yemen	69.4	63.5-72.4	15	Hirth & Carr (1970)
Oman	73.3	60.0-83.0	48	Ross (1981)

a/ Straight carapace length in centimetres unless otherwise noted

b/ Curved carapace length

Table IV

Weights of nesting hawksbill turtles (kg)

Location	Mean	Range	N	Source
Atlantic Ocean				
Nicaragua	54.2	27.2-86.2	32	Nietschmann (1972a)
Puerto Rico	68.4	60.5-76.3	2	Thurston and Wiewandt (1976)
Pacific Ocean				
Solomon Islands	66.3	41.8-77.3	40	McKeown (1977)
Solomon Islands	57.8	36.0-72.5	43	Vaughan (1981)
Australia	49.5	45.5-55-0	8	Limpus (1980)
Indian Ocean				
Democratic Yemen	43.2	35.3-50.0	15	Hirth and Carr (1970)

carapace of the female. The males are very active at this time and may pursue females to the beach; copulation may last several hours. The copulating turtles appear to be preoccupied with the procreative process, and show little response to external stimuli until copulation is complete. Several males may show interest in the same female at the same time, indicating a polyandrous breeding behaviour.

3.1.4 Fertilization

Fertilization is internal.

3.1.6 Nesting process

Beach description: Hawksbills generally prefer to nest on small, isolated beaches, these frequently being on offshore cays, around the world (Figure 4). An exception is the less-shy turtle population in the Solomon Islands (McElroy and Alexander, 1979). The nesting beaches often have barrier reefs with coral and/or rock outcrops, rock and shell debris, fine to course sand, and thick vegetation. Hawksbills have shown a tendency to nest amongst the thick vegetation at the rear of the beach platform (Mortimer, 1981). Descriptions of some representative hawksbill nesting beaches are found in the following sources: Hirth and Carr (1970), Democratic Yemen; Heang (1975), Malaysia; Diamond (1976), Seychelles Islands; McKeown (1977) and Vaughan (1981), Solomon Islands; Hirth and Latif (1980), Sudan; Witzell and Banner (1980), Samoa; Sumertha (1980), Indonesia; Ross (1981), Oman. Photographs of "typical" hawksbill nesting beaches are found in Bustard (1970), Witzell (1974), Heang (1975) and Diamond (1976).

Hawksbills occasionally nest in areas supporting other nesting species of marine turtles, but these beaches are generally much larger, with less obstructions, finer sand and less vegetation than typical hawksbill beaches. In these areas, interspecific nesting habitat is often divided temporally, spatially, or both. Carr, Hirth and Ogren (1966) and Frazier (1979) discussed this niche division for Costa Rican and Indian Ocean nesting Chelonia mydas and hawksbill turtles. Additional hawksbill populations, clearly illustrating interspecific niche division, are described in the following sources: Hornell (1927), Stoddart and Wright (1967), Hirth and Carr (1970), Japanese Tortoise Shell Association (1973), Sumertha (1980) and Ross (1981). According to McElroy and Alexander (1979) and Vaughan (1981), however, there is little or no niche separation between nesting hawksbills and Chelonia mydas in the Solomon Islands.

Nesting season: The nesting season for hawksbills varies considerably according to geographic location (Table II). Nesting seasons often coincide with local rainy seasons when wind velocity drops (Penyapol, 1958, Gulf of Thailand; Harrison, 1969, Sabah; Hirth and Carr, 1970, Gulf of Aden; Bhaskar, 1978, Lakshadweep Islands; Schulz, 1975, Suriname; Diamond, 1976, Seychelles Islands; Garnett, 1978, Seychelles Islands; Frazier, 1979, Seychelles Islands; Witzell and Banner, 1980, Samoa). Nietschmann (1972b) reported that hawksbills in eastern Nicaragua nested during the rainy season, but observed that nesting also coincided with high wind velocities and rough seas. Hawksbill turtles in the Solomon Islands were reported to nest during the calm and monsoon seasons, with heavy rain occurring during both periods (Vaughan, 1981). Diamond (1976), Garnett (1978) and Frazier (1979) suggested that the rain may help consolidate the excavation of the egg chamber, but Harrisson (1969) believed that the low hatching success of hawksbills in Sabah was due to heavy rainfall during the nesting/rainy season. The

prevailing trade winds usually abate during this period and the seas around the nesting beaches become calm, thereby permitting copulation and reef passage free from heavy surf. Also, nest destruction and beach erosion due to large wave surges are at a minimum. Deraniyagala (1939) speculated that there are two peaks in the year-round nesting and two different nesting areas in Sri Lanka, depending on which of the two seasonal monsoons are in progress. The same nesting patterns were also found in the Gulf of Thailand (Penyapol, 1958).

Hawksbills have been reported to nest in the western central Atlantic Ocean every month of the year. However, most nesting takes place April through September. The only accounts of nesting seasons in the eastern Atlantic (Greef, 1884; Eisentraut, 1964) state that nesting occurs in the Gulf of Guinea November through February.

The major nesting months in the islands of the central Pacific Ocean extend September through February and year-round in the western Pacific (Solomon Islands, Philippines, Indonesia, Southeast Asia), with different peak months, depending on exact location.

The nesting season in the Indian Ocean also varies considerably, with local aberrations. In the Seychelles Islands, nesting occurs July through May with November through February as peak months. Nesting takes place in March in the Red Sea and April through June in the Persian Gulf.

Behaviour: Hawksbills are solitary nesters throughout their range, except for the nesting aggregation that Bustard (1972, a, 1973, 1974) reported in the Torres Straits. Hawksbills have been reported to nest during the daytime in the Seychelles (Fryer, 1911; Diamond, 1976; Garnett, 1978; Frazier, 1981) and China (Chu-Chien, 1981), predominantly at night-time in the Torres Straits (Bustard, 1979), Solomon Islands (Vaughan, 1981) Red Sea (Hirth and Latif, 1980), and always at night in Costa Rica (Carr, Hirth and Ogren, 1966), Solomon Islands (McKeown, 1977), Samoa (Witzell and Banner, 1980) and Oman (Ross, 1981). Based on interviews with local fishermen in Indonesia, the Japanese Tortoise Shell Association (1973) reported that hawksbills nest only at night in heavily populated areas but during the day in uninhabited areas.

Hawksbills have shown a tendency to emerge to nest on a rising tide (Nietschmann, 1972b; McKeown, 1977; Garnett, 1978; Ross, 1981), and although Diamond (1976) found no significant correlation between nesting and tides, Garnett (1978) found that significantly more hawksbills nest during periods of neap tides. Also, McKeown (1977) found no relationship between position and brightness of the moon and stars, or the degree of cloud cover, rain, or wind on nesting.

Nesting site selection is apparently a complicated process involving many factors. Garnett (1978) found that hawksbills in the Seychelles avoided exposed reefs as well as areas of beach rock and steep slopes when landing, usually nesting on stable sections of beach under vegetation (preferably Scaevola taccada).

Nesting: A general description of hawksbill oviposition from a single individual nesting in Sri Lanka, lasting 1.75 h, is presented by Deraniyagala (1930, 1939). The nesting process of hawksbills observed in eastern Nicaragua lasted about 1 h (Nietschmann, 1972b). Carr, Hirth and Ogren (1966) illustrated and described in detail the nesting process of Costa Rican hawksbills, which lasts about 2 h. This process is divided into ten stages and is synopsized as follows:

(1) Landfall, stranding and emergence from surf: The turtle is wary and will rapidly return to the sea if disturbed by light or movement. The turtle presses her muzzle against the sand, then lifts her head to peer about the beach, a process that usually lasts through the traversal up the beach until the nest site is selected.

(2) Travel from surf to high beach: The gait up the beach is generally by diagonal limbs working together, with occasional simultaneous movements of paired legs when tired.

(3) Selection of nest site: When dry sand is reached, the turtle presses her muzzle to the ground more frequently and starts to make trial sweeps with the fore flippers. The route to the nesting site is not always direct and may involve considerable zigzags.

(4) Clearing the site and excavating the body pit: When a nest site is selected the turtle makes a few sweeps with its fore flippers, used singly, to clear the site of debris. The hind feet, working alternatively, and alternating with the front flippers, also begin to clear the site, possibly shifting the turtle several inches in any direction. This process may or may not result in a shallow body pit. After several minutes the fore flippers stop and the hind feet begin to scoop out the nest cavity under the tail.

(5) Excavation of the egg cavity: The hind feet continue to work alternatively to dig the flask-shaped hole. The edge of the foot is pressed to the ground, curled to scoop out the sand, then lifted and swung laterally to deposit the sand several inches out from the hind margin of the shell. As this sand is dropped,

the rested foot snaps forward, throwing sand from beside the hole to the front and side, and then repeats the process.

(6) Oviposition: When the cavity is finished the hind feet rest palm down several inches on each side of the hole, the tail is dropped into the cavity, the cloacal opening is everted slightly, and egg extrusion begins. The eggs are generally extruded in twos and threes. As the eggs emerge, the hind feet curl and the head and neck are retracted and bent down, returning to the extended horizontal position on the sand between extrusions. Mocus is frequently secreted between the egg extrusions.

(7) Filling nest: Filling the egg cavity begins immediately after the last egg has been laid; the hind feet then alternately scoop sand from beside the hole and carry it over and dump it in the opening. The tail is repeatedly thrust into the filling cavity and eventually this filling is interrupted from time to time by the kneading of the sand fill with the leading edges of the hind feet.

(8) Filling the body pit and concealing the site: The front flippers begin throwing sand backward, at first alternately, then together, and the pressing action of the hind feet is converted into kicking strokes. This slowly propels the turtle forward, obliterating the nest and leaving a broad zone of disturbed sand.

(9) Return to the sea: The turtle rapidly returns to the sea using the diagonal foot gait, stopping momentarily to press her muzzle to the sand and peer about.

(10) Traversal of the surf: The turtle quickly disappears through the surf.

Minor differences of nesting behaviour were found between the Costa Rican hawksbills and those found in the Gulf of Aden (Hirth and Carr, 1970), the Red Sea (Hirth and Latif, 1980) and Gulf of Oman (Ross, 1981). Diamond (1976) reported that the 2.5 h nesting behaviour of the Seychelles hawksbill is similar to that of Chelonia mydas described by Hendrickson (1958), and McKeown (1977) reported that the nesting behaviour of the Solomon Island hawksbills and Chelonia mydas is also similar. The differences of nesting behaviour in these cases are characteristic between the two genera as compared by Harrisson (1965) and Carr, Hirth and Ogren (1966), and reviewed by Ehrenfeld (1979), Carr (1981) and Hendrickson (1981).

Several large hawksbill populations have shown an unexplained tendency toward aborted nesting attempts (Diamond, 1976; McKeown, 1977; Hirth and Latif, 1980). Garnett and Frazier (1979) reported that fewer unsuccessful nesting attempts per turtle occur in the Seychelles turtles as the nesting season progresses, and Limpus (1980) attributed the many unsuccessful nesting attempts on certain Australian rookeries to coarse beach shingle.

Multiple nesting: Local inhabitants around the world, amateur naturalists, and even some scientists, have reported that the hawksbill turtle nests every two weeks in the nesting season, an exception being the 20-day interval reported in Schmidt (1916). Recent studies have shown this renesting interval to be variable, however, tending more toward a three-week interval. The renesting interval observed from the tag returns of five turtles in eastern Nicaragua indicated an interval of 18.5 ± 2.4 days (Nietschmann, 1972b). Tagging data in Costa Rica (Carr and Stancyk, 1975) have shown that these hawksbills renest after 19 days once or twice a season. Results of similar tagging studies in the Seychelles (Diamond, 1976) indicated that these turtles renest four times per nesting season at 15-18 day intervals, although Garnett and Frazier (1979) report only three clutches per season for the same population. Further studies on Seychelles turtles by Garnett (1978) confirmed the 15-16 day renesting interval. The mean interval of tagged hawksbills renesting in the Solomon Islands was 18 days (McKeown, 1977) and 24.5 days (Vaughan, 1981), the turtles nesting two times per season (McElroy and Alexander, 1979). Ross (1981) reported that Oman hawksbills renest at an unknown interval two-three times per season.

Renesting turtles generally return to the same beach, often to within several metres of their previous nests. Carr and Main (1973), Carr and Stancyk (1975) and Bustard (1979) concluded from observations on colouration, carapace morphology and shell thickness of Torres Straits hawksbills that these individual nesting populations mate and nest faithfully at the same location, even though the nesting islands are only a few kilometres apart. Diamond (1976) and Garnett (1978) found that although Seychelles hawksbills show a strong tendency to return to the same area to renest, some may renest on nearby islands. McKeown (1977) and McElroy and Alexander (1979) suspected that the low tag-return rate in the Solomon Islands may support the local belief that hawksbills are sometimes opportunistic nesters.

There is evidence that some of the hawksbills may nest more than one season, on a 2-3 year cycle, although the majority of turtles apparently only nest once (Hughes, 1981a). See section 3.5.1.

Hawksbill turtle nesting behaviour and biology is reviewed by Hirth (1980) and Ehrhart (1981).

3.1.7 Eggs

Fresh hawksbill turtle eggs are white and spherical with soft, papery shells coated with a mucilaginous secretion. This coating is absorbed after several hours and the shell then takes on a parchment-like texture.

Abnormal eggs, in the form of small yolkless lumps, were found in every nest observed in the Gulf of Aden (Hirth and Carr, 1970), Red Sea (Hirth and Latif, 1980) and Gulf of Oman (Ross, 1981; Ross and Barwani, 1981). Carr, Hirth and Ogren (1966) reported that a variable number of these yolkless lumps may be found in Costa Rican nests (also a few slightly elongate abnormal eggs), Witzell and Banner (1980) found these lumps occasionally in Samoa, and Limpus (1980) rarely found them in Australia.

Hawksbill clutch parameters, such as clutch depth, egg size, and number of eggs per clutch, have been recorded for numerous turtle populations. Depths to the top and bottom of the egg mass were recorded from Costa Rica and Western Samoa (Table V). Also, the egg diameters and weights from nesting populations around the world have been summarized in Tables VI and VII, respectively. The egg mass depths are comparatively uniform and the egg sizes almost identical; however, the number of eggs per clutch (Table VIII) varies considerably and may be correlated with female size. Hirth (1980) reviewed hawksbill nesting biology and found a direct relationship between mean clutch size and mean carapace length of nesting hawksbills from six populations. Ross (1981) suggested that the small clutch sizes of Oman hawksbills may be due to a seasonal cold water upwelling which inhibits turtle growth and the ability to store energy for large clutch sizes. On the other hand, McKeown (1977) believed that there is no apparent correlation between clutch size and turtle size in the Solomon Islands due to the large variation in clutch sizes. Garnett (1978) found no distinct correlation between clutch size and turtle size, concluding that there were probably a wide variety of factors influencing the clutch size.

Hawksbill clutch incubation periods and hatching success, including natural and transplanted clutches, have been recorded for several turtle populations. The incubation periods for different hawksbill populations (Table IX) are fairly consistent, each clutch being subject to individual variation depending on clutch size and prevailing weather conditions (Bustard, 1972; McKeown, 1977; Witzell and Banner, 1980). The incubation period was found to be significantly related to clutch size in the Seychelles, larger clutches incubating faster than small clutches (Garnett, 1978). The length of the clutch incubation period was reportedly longer, accompanied with lower percent emergence rates, in clutches laid during the peak nesting months in the Solomon Islands (Vaughan, 1981). The hatching success of various hawksbill populations is summarized in Table X. Witzell and Banner (1980) opened the unhatched eggs to determine success of fertilization and found that 23 percent of the eggs showed no detectable development. Raj (1976) suggested that the variations of hatching success rates were attributed to the different methods of collecting, transporting and incubation. Experimenting with transplanted eggs in Fiji, Raj (1976) found that a high percentage hatching success is possible on transplanted nests of different ages as long as the eggs are not rotated or physically shocked.

The nest temperature of a clutch incubated in a Fijian laboratory increased 5°C over ambient air temperature (Raj, 1976). Temperatures of incubating hawksbill clutches in Samoa averaged an increase of 3.6°C over ambient sand temperatures at equal depth and were influenced by prevailing weather conditions. Long periods of rain during the early developmental stages prolonged hatching (Witzell and Banner, 1980). Goodwin (1981) found that natural nests had higher temperatures and greater temperature ranges than transplanted nests in Grenada, metabolic heat accounting for an increase of as much as 2.2°C.

Table V

Depths to top and bottom of hawksbill turtle nests (cm)

Location	Mean	Range	N	Source
Depths of top of nests				
Costa Rica	25.4	22.8-30.5	4	Carr, Hirth & Ogren (1966)
Western Samoa	26.9	11.0-36.5	23	Witzell & Banner (1980)
Depths to bottom of nests				
Costa Rica	43.2	43.2-44.4	4	Carr, Hirth & Ogren (1966)
Western Samoa	46.2	34.5-54.9	23	Witzell & Banner (1980)

Table VI

Diameters of hawksbill turtle eggs (cm)

Location	Mean	Range	Nc[a]/	Ne[b]/	Source
Atlantic Ocean					
Mexico	3.6	-	-	12	Marquez (1970)
Costa Rica	3.8	3.5-4.2	5	200	Carr, Hirth & Ogren (1966)
Guyana	-	3.6-4.0	-	-	Pritchard (1969)
Virgin Islands	-	3.9-4.0	1	-	Schmidt (1916)
Pacific Ocean					
Micronesia	-	3.3-3.6	-	-	Nakajima (1920); Fukada (1965)
Western Samoa	3.4	3.4-3.6	23	235	Witzell & Banner (1980)
Philippines	-	3.1-3.5	1	-	Alcala (1980)
Australia	3.6	3.3-3.9	7	70	Limpus (1980)
Indonesia	3.6	3.3-3.9	-	20	Sumertha (1979)
Indian Ocean					
Sri Lanka	3.6	3.5-3.8	1	19	Deraniyagala (1939)
India	-	3.3-3.8	5	-	Bhaskar (1979)
Sudan	4.0	3.7-4.2	2	20	Hirth & Latif (1980)
South Yemen	4.0	3.8-4.5	1	-	Hirth & Carr (1970)

a/ Clutch sample size

b/ Egg sample size

Table VII

Weights of hawksbill turtle eggs (g)

Location	Mean	Range	Nc[a]/	Ne[b]/	Source
Pacific Ocean					
Micronesia	23.0	-	-	-	Nakajima (1920); Fukada (1965)
Philippines	-	20.0-22.0	1	-	Alcala (1980)
Australia	26.4	22.5-30.5	6	60	Limpus (1980)
Indonesia	24.2	20.0-31.6	-	20	Sumertha (1979)
Indian Ocean					
Sri Lanka	26.7	26.2-27.6	1	5	Deraniyagala (1939)

a/ Clutch sample size

b/ Egg sample size

Table VIII

Numbers of hawksbill turtle eggs/nest

Location	Mean	Range	N	Source
Atlantic Ocean				
Costa Rica	161.1	53-206	57	Carr, Hirth & Ogren (1966)
Guyana	158.1	139-176	7	Pritchard (1969)
Surinam	146.0	112-179	13	Schulz (1975)
Puerto Rico	124.0	114-134	2	Thurston & Wiewandt (1976)
Grenada	118.6	54-178	36	Goodwin (1980, 1981)
Pacific Ocean				
Micronesia	104.5	63-151	4	Nakajima (1920); Fukada (1965)
Western Samoa	149.5	60-219	23	Witzell & Banner (1980)
Fiji	116.8	68-168	8	Raj (1976)
Solomon Islands	137.5	75-250	175	McKeown (1977)
Solomon Islands	151.0	37-234	198	Vaughan (1981)
Philippines	121.6	112-130	3	Alcala (1980)
Australia	111.7	62-142	29	Limpus (1980)
Sabah	128	128	1	De Silva (1969)
Malaysia	121.5	80-163	2	Heang (1975)
Gulf of Thailand	115.3	-	224	Penyapol (1958)
Indian Ocean				
Sri Lanka	126.5	115-138	2	Deraniyagala (1930, 1932)
Seychelles	182.0	160-242	9	Diamond (1976)
Seychelles	163.4	-	46	Garnett (1978)
India	135.7	96-177	8	Bhaskar (1979)
Sudan	73.2	32-117	26	Hirth & Latif (1980)[a/]
South Yemen	81.2	69-99	5	Hirth & Carr (1970)[a/]
Oman	97.2	75-118	9	Ross (1981)

a/ See also Hirth (1980)

Table IX

Incubation periods of hawksbill turtle nests[a/]

Location	Mean	Range	N	Source
Atlantic Ocean				
Mexico (S)	60.0	-	-	México, Secretaría de Industria y Comercio (1966)
Costa Rica (T)	58.6	57-74	13	Carr, Hirth & Ogren (1966)
Grenada (T)	75.0	65-82	34	Goodwin (1980, 1981)
Pacific Ocean				
Western Samoa (T)	62.0	59-70	23	Witzell & Banner (1980)
Fiji (T)	63.0	61-66	4	Raj (1976)
Solomon Islands (U)	64.4	43-90	174	McKeown (1977)
Solomon Islands (S)	66.5	49-91	198	Vaughan (1981)
Indian Ocean				
Sri Lanka (T)	62.5	60-65	2	Deraniyagala (1930, 1932)
Seychelles (U)	62.0	56-79	31	Diamond (1976)
Seychelles (S)	59.8	-	50	Garnett (1978)

a/ Incubation period is defined as the interval between egg-laying and hatchling emergence: S = status of nests unreported; T = transplanted nests; U = undisturbed nests

Table X

Percentage of hawksbill turtle eggs resulting in emerged hatchlings[a/]

Location	Mean %	Range %	N	Source
Atlantic Ocean				
Costa Rica (T)	46.7	12-80	9	Carr, Hirth & Ogren (1966)
Grenada (U)	62.2	0-94.1	22	Goodwin (1980, 1981)
Grenada (T)	55.9	1.4-92.5	9	Goodwin (1980, 1981)
Pacific Ocean				
Western Samoa (T)	71.1	35.4-91.8	23	Witzell & Banner (1980)
Fiji (T)	89.2	76.2-100	8	Raj (1976)
Fiji (U)	80.2	-	1	Raj (1976)
Solomon Islands (U)	84.3	57.0-100	179	McKeown (1977)
Solomon Islands (S)	81.7	30.0-100	225	Vaughan (1981)
Australia (U)	91.0	-	18	Limpus (1980)
Sabah (T)	47.3	-	-	De Silva (1969)
Malaysia (T)	47.9	-	-	Heang (1975)
Indian Ocean				
India (U)	96.9	-	-	Bhaskar (1979)
Seychelles (S)	86.0	-	-	Diamond (1976)

a/ S = status of nests unreported; T = transplanted nests; U = undisturbed nests

Ackerman (1980) believed that the gas exchange of hawksbill eggs should follow a pattern similar to Chelonia mydas in that the gas exchange of an incubating clutch, necessary for embryonic growth and hatching success, creates gas partial pressure gradients between the centre and periphery of the clutch and between the clutch and the surrounding beach.

Documented predation on hawksbill eggs is limited. Diamond (1976) and Garnett (1978) found that in the Seychelles, ghost crabs, Ocypode spp. (mainly O. ceratophthalmus), entered many nests to eat eggs, completely destroying some nests. Egg predation by Ocypode spp. and hermit crabs, Coenobita spp., was reported in 19 percent of the hawksbill nests laid in the Solomon Islands, completely destroying about 3.5 percent (Vaughan, 1981). Nest destruction by monitor lizards (Varanus sp.) was reported from Kampuchea (Le Poulain, 1941), Australia (Limpus, 1980), and the Adaman and Nicobar Islands of India (Bhaskar, 1979; Kar and Bhaskar, 1981). Domantay (1953) also found monitors, dogs and ghost crabs preying on hawksbill nests in the Philippines. Possible egg predation by iguanas, rats, pigs and dogs was reported in the literature but is not discussed here because of its speculative nature. Nest destruction by crabs or other animals was not seen in the Red Sea (Hirth and Latif, 1980), Samoa (Witzell and Banner, 1980) and Oman (Ross, 1981) though potential predators were often abundant.

The possibility of hawksbill nest destruction caused by overcrowded nesting beaches is discussed by the Japanese Tortoise Shell Association (1973), and McElroy and Alexander (1979), but only documented from the Seychelles (Garnett, 1978) and Solomon Islands (Vaughan, 1981). Helfman (1968) reported hawksbill nest destruction in Micronesia from water-logged nests filled with roots, and by accidental excavations by incubator birds (Megapode sp.) and land crabs. Accidental excavation of hawksbill nests by nesting Megapodius freycinet has also been reported in the Solomon Islands, as well as a 15-percent nest loss due to storms, high tides and sand displacement (Vaughan, 1981).

3.2 Embryonic and Hatchling Phase

3.2.1 Embryonic phase

Embryological studies on the hawksbill are limited. Deraniyagala (1939) described the general aspects of hawksbill embryological development in a series of stages as follows:

(a) Age = 6 days. Curved length = 8 mm. Embryo open ventrally from below heart-liver mass. Nasal cavities, eyes and otic capsules formed. A pineal prominence on head. Ectodermal branchial grooves well defined and four in number. Maxillary process forms a short peduncle. Limbs form prominences. Allantois bifid and globose. Tail short, thick, and projects over end of body.

(b) Age = 13 days. Curved length = 8 mm. Head and tail flexed toward each other. Joints of elbow and knee defined; limbs with end plates. Carapace outline forms a thick lateral fold. Ectodermal branchial grooves represented by a precervical sulcus. Neck thick and short. Snout nearly touching heart-liver mass, which is almost in middle of length. Eyes globose. Tail thick and elongate.

(c) Age = 21 days. Curved length = 13 mm. Length of carapace = 9.5 mm. No ectodermal branchial grooves. Embryo very thick set, head enlarged and flexed onto cardiac area; Columella auris forms a tympanic prominence. Carapace outline complete both anteriorly and posteriorly. Digits discernible, tail coiled. Embryo recognizable as a testudinate.

(d) Age = 28 days. Length of carapace = 11 mm, width = 6 mm; width of vertebral scute = 4 mm; width of costal scute = 3 mm; length of head = 8 mm, depth = 7 mm, width at eyes = 7 mm; length of tail = 5 mm. Embryo unpigmented except for eyes. Head flexed onto chest; tail cylindrical in section, except for a dorsal ridge, curved toward plastron and with a penultimate kink. Eyelid annular and undeveloped. Eyes very prominent, making head wider than carapace. Rudiments of sclerotic plates present. Columella auris forms a strong prominence. Lower jaw shorter than upper. A lateral fold extends along neck. Carapace scutes discernible, the vertebrals wider than costals, each scute raised into a prominence. No plastral scutes recognizable. Fore limbs longer than hind limbs; digits discernible on all limbs, the inner digit of each projecting beyond the margin of the flipper; specific characters have commenced.

(e) Age = 38 days. Head length = 16 mm, width = 11 mm; carapace length = 30 mm, width = 22 mm; plastral length = 19 mm; length of fore limb = 21 mm, length of hind limb = 14 mm. Carapace with five well defined ridges; plastron with four. Pholidosis and pigmentation complete. Limbs with two claws on anterior pair; sometimes three on each of the hind ones when the third claw is vestigial. Genital prominence partially retracted; animal commencing to flex over yolk. Frontal scale black; frontoparietal with a diffuse dark outline and continued posteriorly as a dark vertebral band along neck and carapace. With the exception of the marginals the carapace scutes are outlined in black. Dorsal is light red. Margin of carapace and posterior margin of limbs white. Nuchal a uniform light red. Two feebly enlarged dark gular scales. Throat dark. Plastron darkening, especially anteriorly, its ridges pale gray.

(f) From 38 days until hatching, an incubation period of 64 days, the embryo is flexed over the yolk, the line of flexure being between the plastral and abdominal scutes. The fore flippers cover the marginal scutes with their posterior edges, the hind flippers are either crossed or placed edge to edge and cover the yolk. Strength of pholidosis, scutation and pigmentation intensified, and ventrally the animal is uniformally black.

Early hawksbill embryonic development, particularly the formation of the amnion, is illustrated and described by Melouk (1949, 1953). He found that the hawksbill differed from other chelonians studied, approaching the highly specialized birds, by the projection of the head and anterior body region above the blastoderm early in the development, the later appearance of the cephalic fold of the amnion, and the relation between it and the tail fold at the time of amnion closure. The hawksbill's general embryology has been described and illustrated (Figure 5) by Voeltzkow (1903), and further embryological work on the skull has been described and illustrated in a series of articles by Fuchs (1907, 1911, 1915). Parsons (1959, 1970) discussed these earlier embryological studies in an extensive review of the subject, reprinting several figures from Voeltzkow (1903) and Fuchs (1915). Also, Fuchs (1931, 1933) described and illustrated the development of certain organs and nerves in the head region of hawksbill embryos and hatchlings.

Goodwin (1981) noted that the greatest embryological mortality in natural and transplanted nests was in the first half of development.

3.2.2 Hatchling phase

Hatchling hawksbills, like other sea turtle genera, move the buried egg chamber to the surface en masse by periodic outbursts of group thrashing, which scrapes sand from the top and sides of the egg chamber, building up the chamber floor until it reaches the surface (Raj, 1976; Carr, 1981). The length and frequency of the periodic thrashing outbursts are dependent upon the diffusion rate of oxygen through the sand to the hatchlings (Raj, 1976). This oxygen diffusion rate may influence the time interval from hatchling to emergence above ground; this interval was found to be six days in Fiji (Raj, 1976) and two days in the Seychelles (Diamond, 1976).

Hawksbill hatchlings in the Seychelles were reported to predominately emerge above ground at night in several small batches 4-6 days after hatching (Diamond, 1976), and Philibosian (1976) reported what appears to be multiple early evening emergences in the Virgin Islands. However, hatchlings have been reported to emerge together explosively in the late afternoon and evening in the Seychelles (Garnett, 1978) and Western Samoa (Witzell and Banner, 1980). Mrosovsky (1968) found that hatchling activity was inhibited by temperatures above 28.5°C and, therefore, the hatchlings emerged at night when sand temperatures cooled. He postulated that this nocturnal emergence keeps the turtles from desiccating in the intense heat on the beach and aids in avoiding terrestrial and airborne predators. Hatchlings emerged in the late afternoons when shadows lowered sand temperatures to about 19°C according to Witzell and Banner (1980).

Upon emergence, hatchlings orient phototropically (Deraniyagala, 1930, 1939; Carr, Hirth and Ogren, 1966; De Silva, 1969), which is presumed to be an innate behaviour to guide them to the sea (Carr, Hirth and Ogren, 1966). Mrosovsky (1970, 1972) found this orientation is an uncomplicated type of tropic reaction, and Philibosian (1976) observed that hatchlings can become disoriented by artificial light sources, which result in mortality from automobiles.

The hatchlings undergo a frenzy of activity lasting several hours after emergence, occasionally all stopping simultaneously to rest for several seconds (Deraniyagala, 1930, 1939). This frenzy is presumably a survival mechanism whereby newly emerged hatchlings can rapidly escape the violent, predator-infested, shoreline environment to the relative safety of the open ocean. The hatchlings initially swim by simultaneous strokes of the fore flippers and diving is reportedly difficult due to the presence of buoyant egg yolk material. Carr (1981), in discussing sea turtle hatchlings in general (presumably including hawksbills), described how the hatchlings traverse the surf zone by diving under incoming breakers and riding the undertow from the preceding wave seaward.

Hawksbill hatchling mortality is high, resulting from physical hardships and predation. Hatchlings were unable to dig their way out of the nest through heavy soil (Diamond, 1976) or root masses (Limpus, 1980), and emergences above ground during the day may lead to immediate immobilization (Carr, Hirth and Ogren, 1966), rapidly followed by death by desiccation (Diamond, 1976). Documented predation on hatchling hawksbills by identified predators is scarce (Table XI). While high mortality undoubtedly occurs due to many species of predators, most authors assume mortality from crabs, dogs, birds, fish and sharks. Countershading, for protection against oceanic predators, is absent in hatchling hawksbills (Bustard, 1976).

Because there is no behavioural information on hawksbill hatchlings once they enter the surf zone, information from captive turtles is of particular interest. Captive hatchlings attempted to dive when stimulated by sharp vibrations through the

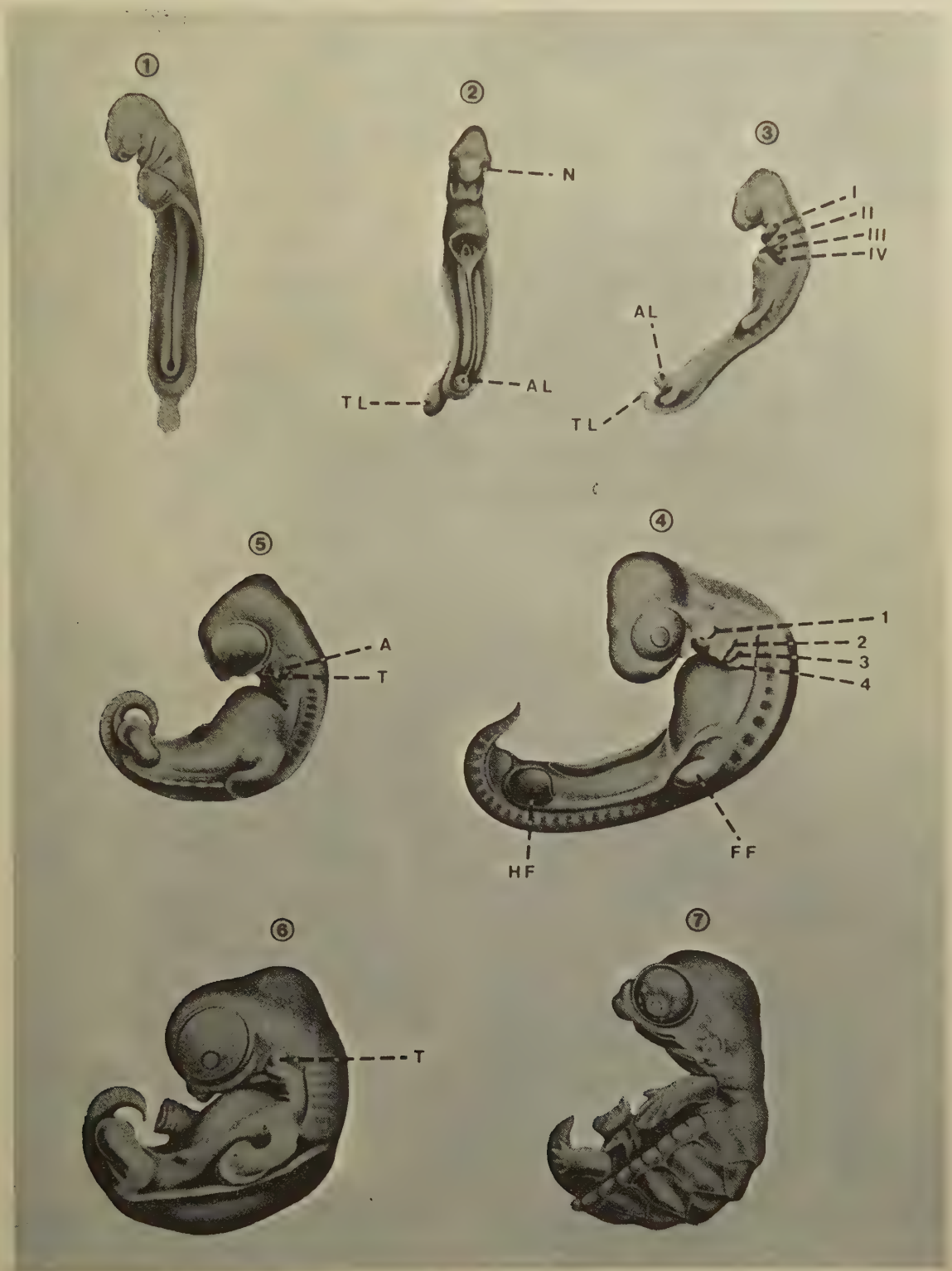

Figure 5 Embryonic development of the hawksbill turtle:
1 - ventral of early embryo (X 9½); 2 - ventral of slightly older embryo (X 9½); 3 - lateral of embryo about eight days old (X 7); 4 - lateral of embryo about ten days old (X 10); 5 - lateral of embryo about 14-20 days old (X 6); 6 - lateral of embryo 24 days old (X 5); 7 - lateral of embryo 35 days old (X 5).
A = auricularhillock; AL = allantois; FF = fore flipper; HF = hind flipper; N - nasal lacuna; T = tympanic protuberance; TL = tail; 1-4 = branchial pouches; I-IV = branchial arches (from Voeltzkow, 1903)

Table XI

Predators of hatchling hawksbill turtles

Predator	Source
Ghost Crabs (Ocypode spp.)	Diamond (1976); Garnett (1978); Bhaskar (1979)
Sharks (Carcharhinus spp.)	Graffe (1873)
Black-Tipped Reef Shark (C. spallanzani)	Trust Territories of the Pacific Islands (1957); Witzell & Banner (1980); Vaughan (1981)
Red Snapper (Lutjanus sebae)	Vaughan (1981)
Sooty Gulls (Larus hemprichii)	Moore & Balzarotti (1976)
Pearly-Eyed Thrasher (Margarops fuscatus)	Thurston & Wiewandt (1976)
Rats (Rattus spp.)	Bhaskar (1979); Kar & Bhaskar (1981)

water (Deraniyagala, 1930, 1939); De Silva, 1969; Goodwin, 1981); presumably this is the functioning of the innate mechanism described by Carr (1981) which enables hatchlings to dive under oncoming surf. Captive hatchlings in Sri Lanka began nibbling seaweed two days after emergence, readily accepting chopped fish when offered (Deraniyagala, 1930, 1939), and Diamond (1976) found captive Seychelles hatchlings begin feeding when four days old. Captive Florida hatchlings rested at night with their fore flippers folded backward on top of the carapace and hind flippers withdrawn (Parrish, 1958).

Hawksbill hatchling abnormalities have been observed at several locations. Aberrant carapace lamination was found in two hatchlings from northeastern Cuba (Grant, 1956), and Deraniyagala (1930, 1939, 1953) observed that carapace scute variations in Sri Lankan hatchlings resulted from eggs laid by a moribund senile turtle. Goodwin (1981) reported that 4 percent of the turtles, hatched in transplanted nests and 1.2 percent, hatched in natural nests in Grenada, had morphological abnormalities: carapace asymmetry, malocclusion of jaws, eyes and limbs that were degenerate, missing or misplaced. Abnormal scale and scute structures were commonly seen in the Solomon Islands (Vaughan, 1981).

Hatchling sizes and weights, like the eggs, are very similar in all populations studied (Tables XII and XIII).

3.3 Juvenile, Subadult and Adult Phase

3.3.1 Longevity

There are no documented longevity estimates for wild hawksbill turtles, although there is the alleged record, summarized by Loveridge and Williams (1957) or 32 years, quoted by Gadow (1901), and traced to Tennant (1861), who quoted Bennet (1843), who followed it back to 1826 and 1794 (Flower, 1925, where full references of preceding citations will be found). Long-term tagging studies of adult females in Costa Rica have shown the maximum time span between first and last observations to be of six years (Carr and Stancyk, 1975). See section 3.4.3.

An aquarium specimen in Berlin was reported by Flower (1937) to be 15 years, 7 months, 28 days old and still alive. Bourlière (1946) estimated the usual longevity at 7-8 years, with an observed maximum of 15 years (probably Flower's).

3.3.2 Hardiness

Schwartz (1961) stated that the hawksbill is a hardy species. This is apparently true only within the preferred circumtropical habitat zones, which it actively seeks when water temperatures drop, while wandering subtropical areas.

Although specimens can be easily reared in captivity, they are prone to bacterial and fungal infections if water quality deteriorates (Deraniyagala, 1939; Kaufmann, 1967, 1972, 1975;

Table XII

Sizes of hatchling hawksbill turtles (cm)

Location	Carapace length	Carapace width	Plastron length	Head width	Source
Atlantic Ocean					
Costa Rica					Carr, Hirth & Ogren (1966)
Mean	4.2	3.1	3.4	1.4	
Range	3.9–4.6	2.7–3.5	3.1–3.7	1.4–1.5	
Sample	41	41	41	41	
Colombia					Kaufmann (1975)
Mean	4.2	3.0	3.2	-	
Range	3.9–4.0	2.8–3.2	3.0–3.4	-	
Sample	25	25	25	-	
Suriname					Pritchard (1969)
Mean	-	-	-	-	
Range	4.1–4.3	2.8–3.2	3.3–3.6	-	
Sample	10	10	10	-	
Grenada					Goodwin (1981)
Mean	4.4	3.1	3.3	1.5	
Range	4.2–4.5	2.9–3.3	3.1–3.4	1.4–1.5	
Sample	319	319	319	319	
Pacific Ocean					
Western Samoa					Witzell & Banner (1980)
Mean	3.9	3.0	3.3	1.4	
Range	3.8–4.1	3.0–3.2	3.2–3.4	1.3–1.4	
Sample	235	235	235	235	
Indian Ocean					
Sri Lanka					Deraniyagala (1932)
Mean	3.9	-	3.0	-	
Range	3.9–4.0	-	3.0–3.1	-	
Sample	3	-	3	-	
South Yemen					Hirth & Carr (1970)
Mean	4.2	3.2	3.2	1.4	
Range	-	-	-	-	
Sample	1	1	1	1	

Table XIII

Weights of hatchling hawksbill turtles (g)

Location	Mean	Range	N	Source
Atlantic Ocean				
Colombia	15.4	13.6-16.9	25	Kaufmann (1972, 1975)
Grenada	17.5	16.3-18.5	319	Goodwin (1981)
Pacific Ocean				
Micronesia	13.0	-	-	Nakajima (1920); Fukada (1965)
Solomon Islands	13.5	-	-	McKeown (1977)
Solomon Islands	13.2	-	120	Vaughan (1981)
Philippines	9.4	8.0-11.0	14	Alcala (1980)
Australia	14.6	12.5-16.0	11	Limpus (1980)
Micronesia	12.3	-	10	McVey (1972)
Sabah	11.4	10.7-12.4	-	De Silva (1969b)
Indian Ocean				
Sri Lanka	14.6	-	2	Deraniyagala (1939)

Japanese Tortoise Shell Association, 1973; and McKeown, 1977). See section 7.

3.3.3 Competitors

The hawksbill is generally an opportunistic omnivore (see section 3.4), foraging over a wide range of reef niches (see section 2.2) with apparently no serious vertebrate competitors. Competition with other marine turtles for nesting sites is minimal and is discussed in section 3.1.

3.3.4 Predators

Predation on hawksbills by carnivorous fish is undoubtedly high, though documented cases are scarce. Cadenat (1957) reported that hawksbills are frequently found in the stomachs of tiger sharks (Galeocerdo arcticus = G. cuvier) of West Africa, and Villiers (1958) stated that Cadenat found four hawksbill skulls in the stomach of a tiger shark (G. cuvier). Randall (1967) found the remains of a juvenile in the stomach of a 155-kg grouper (Epinephelus itajara) from the West Indies, and Pritchard (1977, 1978, 1981a) reported that hawksbill remains were found in the stomachs of six crocodiles (Crocodylus porosus) out of 300 stomachs examined in Micronesia. Juvenile turtles at least 15-cm carapace length released on the beach in Australia attracted black-tipped reef sharks (Carcharhinus spallanzani); these sharks inspected the turtles but did not eat them, the turtles presumably being too large (Bustard, 1979). Vaughan (1981) reported that 24 percent of the nesting hawksbills in the Solomon Islands had predator damage, predation being so common that Japanese tuna longline fishermen cut open shark stomachs to look for turtle shell.

The behavioural defense of an adult hawksbill turtle against a shark attack is described by Vaughan (1981). Apparently, just before the shark attacked, the turtle rotated its body so that the carapace was perpendicular to the angle of attack, and the shark was therefore unable to close its jaws on the hard surface. The turtle did not attempt to escape between attacks and the shark eventually lost interest and left.

3.3.5 Parasites and commensals

Published information containing species of parasites, diseases and commensals is incomplete; identified species are presented in Tables XIV and XV. Numerous parasites and commensals have been reported from Atlantic Ocean hawksbills. Murray (1895) reported encrusting barnacles as well as commensal nudibranchs and crabs from ocean-captured hawksbills in the Atlantic. Carr, Hirth and Ogren (1966) noticed that the shells of Costa Rican turtles are often encrusted with large barnacles and algae, suggesting that this is evidence of a sedentary life, and Pritchard (1969) found most nesting hawksbills

Table XIV

Parasites and commensals reported from hawksbill turtles
(see text for references)

Kingdom - Plantae

Phylum - Schizomycophyta

Family - Entenobacteriaceae

Salmonella regent

Phylum - Cyanophyta

Family - Oscillatoriaceae

Microcoleus lyngbyaceus

Oscillatoria lutea

Spirulina subsala

Schizothrix calcicola

Schizothrix tenerrima

Family - Entophysalidaceae

Entophysalis conferta

Entophysalis duesta

Family - Chroococcaceae

Anacystis dimidiata

Family - Rivulariaceae

Calothrix crustacea

Phylum - Chlorophyta

Family - Chaetophoraceae

Ochlochaete ferox

Phaesophila dendroides

Pilinia sp.

Pseudopringsheimia sp.

Family - Cladophoraceae

Cladophora crystallina

Rhizoclonium implexum

Family - Bryopsidaceae

Bryopsis pennata

Family - Ulvaceae

Enteromorpha clathrata

Table XIV (continued)

Phylum - Rhodophyta

Family - Acrochaetiaceae

Acrochaetium catenulatum

Acrochaetium daviesii

Acrochaetium robustum

Acrochaetium sp. (2)

Family - Ceramiaceae

Ceramium gracillimum

Ceramium serpens

Family - Bangiaceae

Erythrotrichia carnea

Goniotrichum elegans

Family - Corallinaceae

Fosliella sp.

Melobesia sp.

Family - Rhodomelaceae

Herposiphonia tenella

Lophosiphonia scopulorum

Family - Gelidiaceae

Gelidiella sp.

Phylum - Phaeophyta

Family - Ectocarpaceae

Ectocarpus irregularis

Ectocarpus mitchellae

Ectocarpus rhodochortonoides

Family - Sphacelariaceae

Sphacelaria furcigera

Sphacelaria novae-hollandiae

Sphacelaria tribuloides

Table XIV (continued)

Kingdom - Animalia

Phylum - Arthropoda

Family - Coronulidae

Chelonibia testudinaria

Chelonibia caretta

Platylepas hexastylos

Platylepas decorata

Tubicinella cheloniae

Stephanolepas muricata

Family - Lepadidae

Lepas anatifera

Conchoderma sp.

Family - Podoceridae

Podocerus chelonophilus

Family - Grapsidae

Planes minutus

Family - Cancridae

Menippe mercenaria

Phylum - Mollusca

Family - Aeolidae

Aeolis sp.

in Guyana also have large barnacles on their shells. A study of late Tertiary and Pleistocene turtle barnacles, some of which infect hawksbills, is presented by Ross (1963). Several species of worms, usually trematodes, have been reported from the alimentary tract of Atlantic hawksbills by Manter (1954), Caballero (1962), Carr and Stancyk (1975) and Hartog (1980). The most complete trematode study to date in the Atlantic is by Fischthal and Acholonu (1976), who reported finding ten families, 20 genera and 28 species of digenetic trematodes from 14 turtles. Also, Chevreux and Fage (1925) reported amphipods from the base of the tail and flippers, and Clark (1965) reported finding on one individual a possible parasitic crab.

Numerous parasites and commensals have been reported from Pacific Ocean hawksbills. Steinbeck and Ricketts (1941) found evidence of barnacles and hydroids on the carapace of an individual hawksbill subadult from the Gulf of California, and Carr (1952) illustrated the susceptibility of Pacific hawksbills to encrusting barnacles in several photographs of specimens from the Bay of Fonseca, Honduras. An adult dead specimen found in Hawaii had several large barnacles and unidentified episodic algae on the carapace, plastron and flippers (Balazs, 1977). Barnacles and algae are frequently found encrusted on turtles from the Solomon Islands (McKeown, 1977; Vaughan, 1981) and Australia (Cogger and Lindner, 1969; Bustard, 1976). The most definitive work to date on barnacles in the Indo-Pacific area was by Monroe and Limpus (1979), who described 17 species of barnacles from five species of sea turtles (including hawksbill) in Australian waters, providing a summary of previous

Table XV

Trematode worms reported from hawksbill turtles
(see text for references)

Pronocephalidae	Angiodictyidae
Pleurogonius laterouterus	*Octangium sagitta*
Pleurogonius linearis	*Octangium travassosi*
Pleurogonius longibursatus	*Octangium microrchis*
Pleurogonius ozakii	*Angiodictyum posterovitellatum*
Pleurogonius puertoricensis	Pachypsolidae
Pleurogonius solidus	*Pachypsolus puertoricensis*
Pleurogonius trigonocephalus	*Pachypsolus ovalis*
Cricocephalus albus	Plagiorchiidae
Cricocephalus americanus	*Enodiotrema reductum*
Cricocephalus megastomus	*Styphlotrema solitarium*
Glyphicephalus latus	Rhytidodidae
Glyphicephalus lobatus	*Rhytidodes gelatinosus*
Epibathra stenobursata	*Rhytidodes indicus*
Pyelosomum posterorchis	Calycodidae
Diaschistorchis pandus	*Calycodes caborojoensis*
Metacetabulum invaginatum	Telorchiidae
Medioporus macrophallus	*Orchidasma amphiorchis*
Adenogaster serialis	Paramphistomidae
Spirorchiidae	*Schizamphistomum scleroporum*
Amphiorchis caborojoensis	Gorgoderidae
Amphiorchis amphiorchis	*Plesiochorus cymbiformis*
Learedius orientalis	
Hapalotrema synorchis	

taxonomic studies on the subject and a key for their identification. Heang (1975) published a photograph of an individual hawksbill from Malaysia that had many barnacles on the head and carapace, and in Indonesia, hawksbills as small as 12.5 cm showed traces of barnacle infestation (Japanese Tortoise Shell Association, 1973). Oguro (1936) described several species of trematodes from hawksbills captured in Japanese waters. Cribb (1969) identified four classes, 26 genera and 30 species of algae from an Australian hawksbill.

Numerous parasites and commensals have been reported from Indian Ocean hawksbills. According to Deraniyagala (1930, 1932, 1939), a nesting female hawksbill in Sri Lanka had encrusting barnacles on the shell and flippers. He said that these turtles often become covered with algae and that even specimens as small as 29 cm are subject to cirripede infestation. Hirth and Carr (1970) found that most adult hawksbills in the Gulf of Aden were encrusted with barnacles on both the carapace and plastron and about half were also encrusted on the head and flippers. Frazier (1971) observed that specimens at Aldabra Atoll

in the Seychelles were much less encrusted than Chelonia mydas; one juvenile had red encrusting algae and two other juveniles had green algae. Diamond (1976) reported that nesting turtles at Cousin Island were often encrusted with at least some type of barnacle, pink or green algae, or brown filamentous algae. Ross (1981) found that most nesting hawksbills in Oman had barnacles on the carapace, also observing many juveniles and subadults encrusted with barnacles, bryozoans, and algae. Descriptions of some species of encrusting barnacles on Indian Ocean hawksbills are given by Nilsson-Cantell (1932) and Daniel (1962). Several species of trematodes are described from hawksbills captured in Indian waters by Simha and Chattopadhyaya (1969) and Chattopadhyaya (1972). Keymer, Ridealgh and Fretwell (1968) described a new species of Salmonella bacteria from an adult male hawksbill captured in Aden.

3.4 Nutrition and Growth

3.4.1 Feeding

The hawksbill turtle appears to be an omnivorous scavenger, its narrow, sharp beak being an excellent adaptation for foraging among coral crevices. Also, the smooth or slightly serrated lower jaw and lack of strongly elevated ridges on the upper jaw reflect the hawksbill's adaptations for omnivority (Mahmoud and Klicka, 1979).

McElroy and Alexander (1979) found that, although hawksbill and Chelonia mydas turtles largely overlap habitats, their feeding areas were spatially separated, the hawksbill preferring to forage the outer edge of fringing reefs and deep lagoons.

Information on the feeding behaviour of hawksbills is scarce and is limited to observations on captive specimens. Deraniyagala (1930, 1939) reported that two-day old captive hatchlings nibbled pieces of seaweed and also seized chopped fish, which they tore into bite-sized pieces using their front flippers. Several of these hatchlings starved because of their inability to dive deep enough to retrieve the fish from the bottom of the tank, due to the presence of buoyant egg yolk material. Witzell (personal observations) observed that the captive Western Samoan hatchlings were always diurnal feeders, becoming inactive at night. Deraniyagala (1939) reported that a captive turtle of unspecified size immediately seized small crabs placed in the tank, but the turtle manoeuvred for a position from which it seized large crabs when they moved, thereby avoiding their claws. He also observed that this turtle was principally a diurnal feeder, feeding at night only when electric lights illuminated the tank. Harrisson (1965) observed that captive juvenile hawksbills used their fore flippers extensively for rasping food. Adult specimens, kept in large public aquaria, moved to about 10 cm from a morsel of food and thrust their heads forward to snap it up, the food masticated and worked to their throats by repeatedly opening the mouth and thrusting the head forward (Parrish, 1958).

3.4.2 Food

Little is known about the diet of wild juvenile, subadult and adult turtles and nothing is known about the diet of wild hatchlings. Varying amounts of both plant and animal matter are often found in hawksbill stomachs. Food items from gut content analysis of wild turtles (Tables XVI and XVII) indicate the hawksbill's opportunistic feeding behaviour, with possibly a preference for benthic invertebrates. However, Hartog (1980) found large quantities of both sea anemone and undigested plant matter in the alimentary tract of a juvenile specimen in the eastern Atlantic and concluded that hawksbills were carnivores, with no, or a very limited, ability to break down cellulose or lignine.

An interesting aspect of the gut content analyses, particularly by Carr and Stancyk (1975), was the presence of large amounts of non-biological materials such as stones, shell, mud and pieces of plastic; raising intriguing questions as to the nature of the hawksbill's feeding mechanism.

Captive specimens will feed on a wide variety of fish, invertebrates and plants (see section 7).

3.4.3 Growth rate

Age and growth studies of the hawksbill have generally been limited to speculation and to sporadic measurements of captive turtles at known age over short time periods. Schmidt (1916) speculated, based on limited data, that hawksbills in the Virgin Islands grew to about 4-5 cm in the first autumn, 7-8 cm in the winter, 10 cm in the spring, and 20 cm in the second autumn. Villiers (1958) felt that hawksbills were fast growers, obtaining 15 cm in five-six months and 40 cm in three years. More recently, Bustard (1973) found that captive reared Australian turtles could attain lengths between 23 cm and 30.5 cm within a year. Based on length frequency distributions of juveniles captured for stuffing, Kajihara and Uchida (1974) and Uchida (1979) felt that

Table XVI

Food identified from hawksbill turtle stomachs

Location	Food	Source
Atlantic Ocean		
Salvage Islands		Hartog (1980)
juvenile	- Coelenterata (Anemonia sulcata; Velella velella; algal hydroid; Siphonophora; Hydromedusae)	
	- algae (Stypopodium zonale; Sargassum vulgare; Dictyota sp.; Cyanophyta	
	- Gastropoda (Littorina striata; Amyclina pfeifferi; Janthina sp.)	
	- Cephalopoda (Taonius pavo; Histioteuthis sp.; Oegopsida)	
	- sponges (2 species)	
	- spider crab (Inachus sp.)	
	- sea urchin	
	- stones	
	- plastic	
Ascension Island		Carr & Stancyk (1975)
adults	- sponge (Ircinia fasiculata)	
Costa Rica		Carr, Hirth & Ogren (1966)
adult male	- sponge (probably Geodia gibberosa)	
adult male	- sponge (probably Geodia gibberosa)	
	- ectoprocts (Amthia; Steganoporella; calcareous species)	
	- hydroid (like Sertularia)	
	- sea urchin spines	
Pacific Ocean		
Magdalena Bay		Steinbeck & Ricketts (1941)
subadult	- red crab (Pleuroncodes planipes)	
Honduras		Carr (1952)
2 specimens	- red mangrove fruit	
1 specimen	- mangrove leaves	
	- dead bark	
	- wood	

Table XVI (continued)

Location	Food	Source
Hawaii		Balazs (1977)
adult female	- sponge (3 kinds)	
New Zealand		McCann (1966)
adult	- barnacles	
	- cephalopods	
	- Velella	
	- Salpa	
	- Spirula (probably dead in association with the barnacles)	
Philippines		Alcala (1980)
2 specimens	- sea grass	
	- sponges	
	- brown algae (Echeuma; Codium)	
Australia		Limpus (1979)
subadults, adults	- ascidians	
	- other encrusting animals	
	- algae	
Formosa		Swinhoe (1863)
juvenile	- algae	
	- shell	
	- black stone	
Indian Ocean		
Sri Lanka		Deraniyagala (1930, 1939)
adult female	- algae	
	- coral	
	- gastropods	
adult female	- ascidian	
Seychelles		Hornell (1927)
adults	- Sargasso weed	
Seychelles		Frazier (1971)
adult female	- sponge	
Seychelles		Fryer (1911)
adults	- algae	
Oman		Ross (1981)
2 specimens	- sponge	
South Yemen		Hirth & Carr (1970)
adult female	- green algae	

Table XVII

Food identified from the stomachs of 29 Costa Rican hawksbill turtles captured between mid-July and early October (from Carr and Stancyk, 1975)[a/]

Food item	Males with		Females with		Unsexed		% of turtles with food in gut (20)	% of all turtles (29)
	No.	%	No.	%	No.	%		
Bottom material	4	36.4	5	38.4	2	40	55.0	37.9
Terrestrial plant material	4	36.4	5	38.4	1	20	50.0	34.5
Plastic and manmade litter	2	18.2	2	15.3	0	—	20.0	13.8
Unidentifiable matter	1	9.1	1	7.7	0	—	10.0	6.9
Marine algae - *Sargassum*	2	18.2	1	7.7	0	—	15.0	10.3
Marine angiosperms								17.2
Thalassia sp.	2	18.2	2	15.3	1	20	25.0	17.2
Syringodium sp.	1	9.1	0	—	0	—	5.0	3.5
Porifera							95.0	65.5
Demospongia								
Poecilosclerina	1	9.1	0	—	0	—	5.0	3.5
Epipolasida	0	—	1	7.7	0	—	5.0	3.5
Hadromerina	1	9.1	1	7.7	0	—	10.0	6.9
Carnosa								
Chondrilla nacula	0	—	1	7.7	0	—	5.0	3.5
other	1	9.1	0	—	0	—	5.0	3.5
Choristida							90.0	62.1
Craniella sp.	0	—	1	7.7	0	—	5.0	3.5
Geodia gibberosa	10	90.9	4	30.7	4	80	90.0	62.1
other	4	36.4	1	7.7	0	—	25.0	17.2
Coelenterata								
Octocorallia	1	9.1	0	—	1	30	10.0	6.9
Hydrozoa	0	—	2	15.3	1	20	15.0	10.3
Bryozoa							35.0	24.1
Schizoporella sp.	1	9.1	0	—	0	—	5.0	3.5
Hippoporina sp.	1	9.1	0	—	0	—	5.0	3.5
other	2	18.2	1	7.7	2	40	25.0	17.2

a/ The parasites (trematodes) found by Carr and Stancyk in the hawksbill stomaches are not included in this table

Table XVII (continued)

Food item	Males with		Females with		Unsexed		% of turtles with food in gut (20)	% of all turtles (29)
	No.	%	No.	%	No.	%		
Mollusca							35.0	24.1
Pelecypoda	4	36.4	1	7.7	0	—	25.0	17.2
Gastropoda	2	18.2	1	7.7	1	20	20.0	13.8
Scaphopoda								
Dentalium laqueatum	1	9.1	0	—	0	—	5.0	3.5
Urochordata								
Ascidiacea							70.0	48.3
Styela sp.	7	63.6	4	30.7	3	60	70.0	48.3
other	2	18.2	1	7.7	0	—	15.0	10.3
Empty	1	9.1	7	53.8	1	20	45.0	31.0

wild hawksbills grew to about 20 cm in one year, 35-40 cm in two years and 60-65 cm in three years. The values of the captive age and growth studies plotted in Figures 6 and 7 indicate rapid growth. However, these studies were frequently plagued with small sample sizes (sometimes a single individual), poor rearing conditions, overfeeding and disease. Because of these problems, growth studies of captive animals do not necessarily represent natural growth rates. A review and discussion of hawksbill age and growth studies was presented by Witzell (1980). A von Bertalanffy growth equation was also presented by Witzell (1980), who suggested that this type of analysis may be more useful if properly designed captive studies are conducted (Table XVIII).

Based on recaptures of tagged Australian turtles, Limpus (1979) found that hawksbill growth rates were similar to those of *Chelonia mydas* and *Caretta caretta*. Kowarsky and Capelle (1979) found that two tagged pond-reared hawksbill juveniles in northern Australia also grew well in the wild. The results of both tagging studies are summarized in Table XIX.

Studies involving the analysis of annular striations in hawksbill hard-parts is a promising field of study. Distinct bands, possibly representing annual growth, have been reported on the carapace lamina in Hawaiian hawksbills (Balazs, 1977). Hohn and Frazier (1979) found conspicuous growth layers in a variety of bones, scutes and keratin in all sizes of hawksbills examined. The number of these layers was related to shell size, except that the number in keratin may exceed that in bone, and the number of layers only indicated the minimum estimate of age because of bone resorption and the wearing down of keratin.

Other growth parameters are the length:weight relationships presented by Hughes (1974), McElroy and Alexander (1979) and Uchida (1979, 1980) for hawksbill populations in South Africa, Solomon Islands and Indonesia, respectively (Table XVIII).

Morphometric analysis of hawksbills was presented by Witzell (1980) for the mean monthly values of captives in Samoa, and data are supplied by Hughes (1974: Figures 24-26) and Uchida (1980: Figure 4) for the morphometric regression analysis of African and Indonesian specimens (Table XX). The methods of analysis of these growth and morphometric data have been standardized whenever possible for comparison (Tables XVIII and XX). Witzell (1980) urged uniform analysis of morphometric data for population comparisons by analysis of covariance techniques. Morphometrics of wild turtles, generally adult females, are not all included for discussion in this section because of the limited size range of specimens usually measured (see section 1.3).

3.4.4 Metabolism

There are no published data on hawksbill turtle metabolic rates, although the normal range between sleep and active swimming must be great.

Dantzler and Holmes (1974) described the salt glands as substantially large organs located in the orbit, consisting of branching

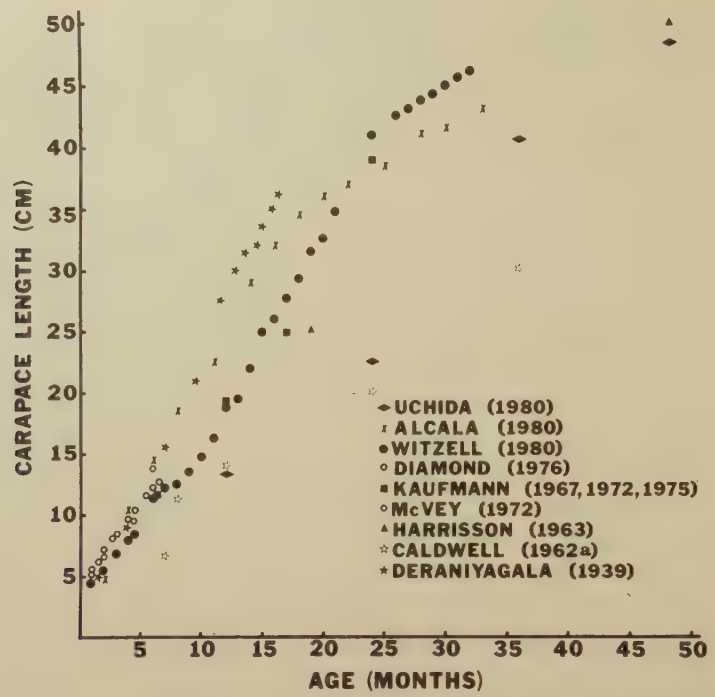

Figure 6 Growth rate (length) of captive hawksbill turtles

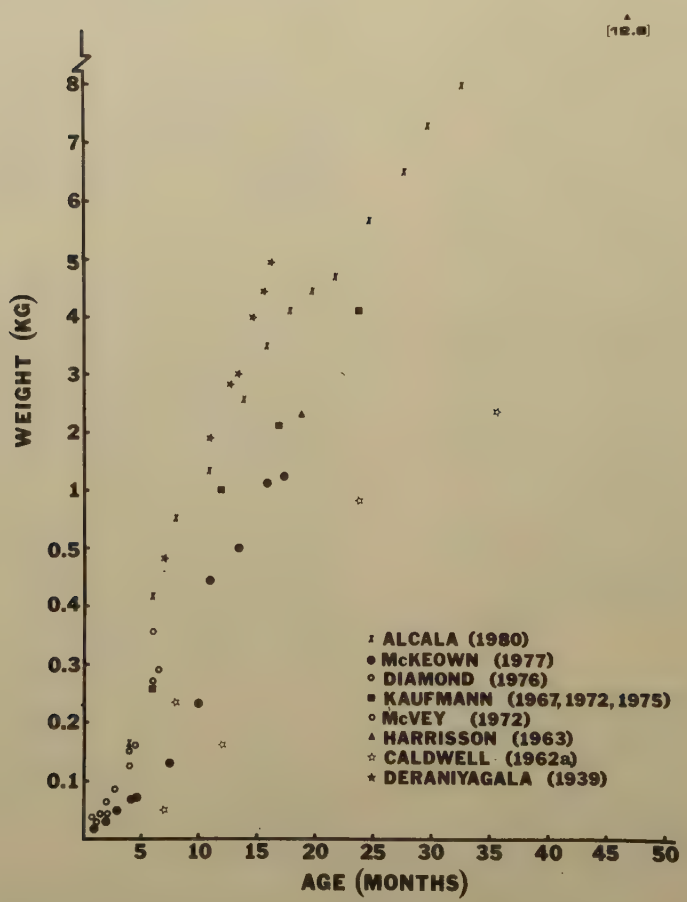

Figure 7 Growth rate (weight) of captive hawksbill turtles

Table XVIII

Growth equations of hawksbill turtles[a/]

Parameter	Equation	N	r	Living status	Size class[b/]	Source
Western Samoa						Witzell (1980)
Age-Growth (months) (cm)	$L = 53.24\ (1-1.8258e^{-0.02035t})$	-	-	captive	H,J,S	
Solomon Islands						McElroy & Alexander (1979)
Weight-Length (kg) (cm)	$W = 0.000108L^{3.0278}$	90	0.99	wild	J,S,A	
Weight-Length (kg) (cm)	$W = 0.000111L^{3.018}$	48	0.96	wild	J,S	
Weight-Length (kg) (cm)	$W = 0.006994L^{2.077}$	42	0.79	wild	Af	
Age-Weight (days) (g)	$W = 18.17e^{0.0094t}$	-	0.99	captive	H,J	
Indonesia						Uchida (1980)[c/]
Weight-Length (kg) (cm)	$W = 0.00045L^{2.63}$	82	0.99	captive	J,S	
South Africa						Hughes (1974)
Weight-Length (kg) (cm)	$W = 0.0007L^{2.63}$	23	-	wild	J,S,A	

a/ Weight = total weight; length = straight line carapace length

b/ H = hatchlings; J = juveniles; S = subadults; Af = adults (females); A = adults (both sexes)

c/ Log linear regression of Uchida (1980) converted to power curve for comparative purposes

Table XIX

Growth results from hawksbill turtle tag and recapture studies in Australia

Initial length (cm)	Months free	Length increment (cm)	Growth rate cm/month	Source
curved carapace				Limpus (1979)
81	48	6.5	0.135	
67	17	2.5	0.147	
straight carapace				Kowarsky & Capelle (1979)
25.4	5	4.1	0.820	
22.9	6.5	4.6	0.707	

Table XX

Morphometric relationships between selected hawksbill body parameters and carapace length (straight line measurements in cm)

Parameter	Relationship to carapace length (CL)	N	r^2	Size class[a/]	Source
Western Samoa					Witzell (1980)[b/]
Carapace Width	$Y = 1.473 + 0.724X$	10	0.99	H,J,S	
% CL	$Y = 81.191 - 0.092X$	10	0.58	H,J,S	
Plastron Length	$Y = 1.446 + 0.693X$	10	0.99	H,J,S	
% CL	$Y = 81.133 - 0.148X$	10	0.92	H,J,S	
Head Width	$Y = 0.775 + 0.135X$	10	0.99	H,J,S	
% CL	$Y = 40.418 - 6.56 \log_e X$	10	0.86	H,J,S	
Eye Width	$Y = 0.404 + 0.35X$	10	0.97	H,J,S	
% CL	$Y = 14.871 - 2.70 \log_e X$	10	0.90	H,J,S	
Indonesia					Uchida (1980)[c/]
Carapace Width	$Y = 1.380 + 0.73X$	82	0.97	J,S	
Plastron Length	$Y = 0.390 + 0.76X$	82	0.97	J,S	
South Africa					Hughes (1974)[c/]
Carapace Width	$Y = 2.871 + 0.788X$	32	0.96	J,S,A	
Plastron Length	$Y = -1.751 + 0.854X$	19	0.98	J,S,A	
Head Width	$Y = 1.003 + 0.128X$	20	0.98	J,S,A,	

a/ H = hatchlings; J = juveniles; S = subadults; A = adults (both sexes)

b/ Sample size is 10 data points representing mean values of several turtles

c/ Data for regression analysis extrapolated from Hughes (1974: Figures 24-26) and Uchida (1980; Table 1)

tubules radiating from central ducts that open to the exterior by a short duct in the posterior corner of each eye. Under natural conditions, the salt glands function intermittently, in conjunction with the kidneys, most commonly in response to food and seawater ingestion. It is possible that turtles may drink sea water to gain sodium as a vehicle for the extrarenal excretion of potassium in food. Furthermore, extrarenal excretion of sodium in a salt-loaded turtle may be influenced by adrenocortical hormones.

Hirth (1962) measured cloacal temperatures of two Caribbean hawksbills, shortly after the turtles laid eggs, and found that their body temperatures differed little from ambient sea temperature.

3.5 Behaviour

3.5.1 Migrations and local movements

One of the classic cases of homing and migration is that of a hawksbill allegedly tagged with a brass ring in 1794 which reportedly revisited the same site in Sri Lanka for 32 consecutive years (discussed in Flower, 1925, and Loveridge and Williams, 1957).

Hawksbill tagging studies are incomplete, but results have produced evidence of both long- and short-distance movements. In the Atlantic Ocean, hawksbill tagging studies have generally been limited to Central America and adjacent areas. Carr, Hirth and Ogren (1966), updated by Carr and Stancyk (1975), saw no clear-cut reproductive migratory pattern in Costa Rican hawksbills. However, they presented circumstantial evidence (mainly tagging results) that limited adult migratory travel may occur from the nesting beach to banks offshore Costa Rica and to Nicaraguan cays by some segment of the nesting population. Nietschmann (1972b) reported that three adult females, tagged in eastern Nicaragua, were recaptured on nesting beaches, two nearby and one in Jamaica. He also reported that an adult male, also tagged in Nicaragua, was later recaptured in Panama. Pritchard (1969, 1976) obtained one short-distance tag return in a small tagging study in Guyana, and Thurston (1976) thought that repeated sightings of individual turtles in Puerto Rico suggested residency.

In the Pacific Ocean, hawksbill tagging studies have been limited to several western Pacific locations. A tagging study in the Solomon Islands had 2-3 percent recaptures, all within 30 mi and six months of release, suggesting a fairly non-migratory population (McKeown, 1977). Based on a hypothetical population model of these Solomon Islands hawksbills, McElroy and Alexander (1979) believe that a significant number may migrate to feed elsewhere. Meylan (1981) and Pritchard (1981) reported that an individual tagged in the Solomon Islands was recaptured in Papua New Guinea. The results of the hawksbill tagging studies in the Solomon Islands were updated by Vaughan (1981) who concluded that at least some nesting turtles may migrate long distances. Kowarsky and Capelle (1979) reported that two pond-reared juvenile hawksbills, tagged in northern Australia, were recaptured in Papua New Guinea. De Silva (1981) reported that one hawksbill turtle, tagged in Sabah, was recaptured in the Philippines after averaging 18 km/day for 713 km. In the Philippines, two tagged hawksbills were recovered locally within 1.5 months from the release dates (Alcala, 1980). In the Indian Ocean, hawksbill tagging studies have been limited to the Seychelles, where turtles, tagged at Cousin Island, had all been recaptured a short distance away (Garnett, 1978; Frazier, in press).

Long-term tagging studies have shown that some hawksbills exhibit cyclic reproductive migrations. Costa Rican studies have produced some evidence that suggests that there is a three-year renesting migration for some of these turtles. Garnett (1978) and De Silva (1981) also reported limited tagging evidence which indicates a two-three year renesting cycle for some of the turtles. Hughes (1981a) reviewed worldwide tag and recapture data as evidence of nesting cycles, concluding that most turtles only nest once because of scant return data.

Maylan (1981) reviewed worldwide hawksbill migratory behaviour from tag and recapture data and concluded that there was not enough evidence to determine the degree to which hawksbills migrate. (See also section 2.2.2.)

3.5.2 Schooling

Hawksbill turtles appear to be solitary animals that do not form into behaviourly similar "schools" or "flotillas" in the classical sense. However, they may form local concentrations or what amounts to aggregations near nesting beaches during the breeding season. The only extant breeding aggregation was reported by Bustard (1972, a, 1973, 1974) in the Torres Straits. Breeding aggregations may have been fairly common in other major undisturbed nesting areas, such as Solomon Islands (McElroy and Alexander, 1979).

3.5.3 Responses to stimuli

The hawksbill turtle has been called an aggressive and pugnacious species (Schwartz, 1961), an unfair accusation considering that this behaviour apparently refers to individuals that were just harpooned, netted, or otherwise molested in their natural environment. True (1893) reported that United States fishermen had to be careful because captured hawksbills bit severely, inflicting painful wounds, and Deraniyagala (1930, 1939) found that hawksbills

defended themselves by biting with vigorous snaps in Sri Lanka. Caribbean turtles also snap and bite furiously (Carr, 1952) when captured and must be subdued with clubs before being boated, as illustrated by the harpooned specimen in Carr, Hirth and Ogren (1966), and Carr (1967). In Malagasy, Loveridge and Williams (1957) found that fishermen protect their fragile craft from considerable damage by holding out a piece of wood for harpooned hawksbills to fasten their jaws into.

When laying eggs, female hawksbills are docile in Sri Lanka (Deraniyagala, 1939), in Costa Rica (Carr, Hirth and Ogren, 1966) and in Guyana (Pritchard, 1969).

While hawksbills spend some of their time either resting or sleeping wedged into coral or rock ledges, usually at night. Bacon and Maliphant (1971) reported several "dormitory" areas in Trinidad, and specimens have commonly been seen resting in Indonesia and the Philippine Islands (Japanese Tortoise Shell Association, 1973; Alcala, 1980). Sleeping hawksbills have been commonly seen in eastern Nicaragua (Nietschmann, 1971), Puerto Rico (Carr, 1977), Micronesia (Faulkner, 1978) and the Solomon Islands (McKeown, 1977; Vaughan, 1981).

Captive West African specimens of unknown size were said to be touchy, irascible and viciously attacked and bit all other animals, even their own species (Villiers, 1958, 1962). Juveniles kept in Sarawak were reported to quarrel over food but were otherwise amiable (Harrisson, 1965). They were reported to be cannibalistic in Indonesian culture ponds (Japanese Tortoise Shell Association, 1973). Uchida (1980) also reported that large numbers of hatchlings and juveniles, reared in Indonesia, suffered bite wounds on their flippers. Hornell (1927), McVey (1972) and Carr and Main (1973) found that young hawksbills could be raised in captivity in the Seychelles and South Pacific, but must be of similar size and not be overcrowded to mitigate injuries due to their aggressiveness. Some comparisons of general captive behaviour patterns of juvenile Indonesian hawksbill, Chelonia mydas and Caretta caretta turtles are given by Harrisson (1965).

Observations on captive adult hawksbills may reflect some behaviour patterns of wild turtles. Published observations are limited to those of Parrish (1958) who observed that adult specimens,kept in large public aquaria with fish and other turtle species, were generally docile, with one observed fight over food and the customary bite when regaining a favourite resting place. Locomotion observed was either by swimming or by crawling (using alternating limbs) and vigorous scratching on debris was seen on numerous occasions. Resting turtles surfaced for air every 10-56 minutes, and active turtles surfaced every 30 seconds to 10 minutes. However, at night the turtles surfaced every 35-45 minutes. After periods of activity or short-term submergences turtles would surface for a single breath, but would take 5-11 breaths at intervals of 5 seconds to 3 minutes, if they stayed down longer than 10-15 minutes. Home ranges were observed for swimming, resting and sleeping activities, the degree and duration varies with individuals. There were four basic resting positions: full juvenile - with the fore flippers positioned flat on the carapace and the hind flippers held close together; semi-juvenile - with the fore flippers extended laterally and the hind flippers held close together; semi-juvenile - with the fore flippers positioned flat on the carapace and the hind flippers extended laterally; spread-eagle - (most common) with all four flippers extended laterally. During rest periods, the head was usually wedged into a crevice and the turtle remained alert with open eyes. Sleeping with eyes closed began soon after sundown and turtles were never seen resting or sleeping on the surface.

4. POPULATION

4.1 Structure

4.1.2 Age composition

There is no information available on the age compositions of hawksbill turtle populations. Estimates of age to maturity of captive specimens range from 3 to 4.5 years and are presented in section 3.1.2; maximum age is discussed in section 3.3.1.

4.1.3 Size composition

There is no information available on the size composition of hawksbill populations. Size ranges of nesting females vary conciderably between populations (Table III) and various growth parameters are discussed in section 3.4.3 and presented in tables 18 and 20.

4.2 Abundance and Density

4.2.1 Average abundance and density

The average abundance and density of hawksbill turtles throughout the oceans are unknown, although it is generally accepted that most nesting populations are declining due to overexploitation (see section 5) and nesting habitat destruction (see section 4.3.2). Possible exceptions are the seemingly large and stable populations in Yemen (Hirth and Carr, 1970), northeastern Australia (Bustard, 1972, a, 1973, 1974; Limpus, 1980), the Red Sea (Hirth and Latif, 1980) and Oman (Ross, 1981).

The numbers of reproductively active female turtles for various nesting hawksbill populations have been estimated by scientists (see pertinent references in section 3), but these numbers are not discussed here because

of their apparent unreliability and dynamic nature. Estimation of population sizes of nesting females by aerial surveys is difficult, since tracks in the sand are short-lived and difficult to see, and hawksbill nests are often obscured by beach vegetation (Meylan, 1981a).

4.2.2 Changes in abundance and density

Although hawksbills are often seen year-round on reefs adjacent to nesting beaches, there are some changes in abundance and density apparently due to reproductive movements (see sections 2.2, 2.3 and 3.1.6). There may also be natural population fluctuations due to annual reproductive success rates. However, in most areas, there is a general decline in hawksbill numbers due to habitat destruction (see section 4.3.2) and increasing harvesting pressure (see section 5). The relative status of hawksbill populations around the world is reported in Björndal (1981).

4.3 Natality and Recruitment

4.3.1 Reproduction rates

The parameters affecting the reproductive rate of the hawksbill turtle appear to vary between nesting populations (see section 3). However, a range of 209-313 hatchlings/female/season has been estimated in Table XXI from reproductive data in section 3. This range of reproductive rate (209-313 hatchlings/female/season) is an overall estimate and is somewhat higher than the figures estimated by Hirth (1980) for Costa Rica and the Seychelles (77-189, respectively). This is undoubtedly due to the larger sample sizes used for the reproductive parameters in estimating the overall reproductive rate in Table XXI.

4.3.2 Factors affecting reproduction

The relatively small mean adult female sizes and small clutch sizes of Yemen and Oman hawksbills may be due to the presence of a cold upwelling along the coast, the cold water inhibiting overall turtle growth and the ability to store sufficient energy for large egg clutches (Ross, 1981).

General environmental factors prevailing during the nesting season (monsoons, temperature, rain and wave surge), as well as specific environmental factors affecting nesting emergence (tide, moon phase and time of day), all affect hawksbill reproduction and are discussed in section 3.1.6. Factors affecting incubation period and nest success (rain, predators, interspecific and intraspecific nest destruction) also affect reproductive success and are discussed in section 3.1.7.

Female hawksbill turtles are disturbed by light and moving shadows (persons, animals, trees) in the early stages of nesting; these disturbed animals rapidly return to the sea (Carr, Hirth and Ogren, 1966; Hirth and Carr, 1970; Diamond, 1976; McKeown, 1977; Hirth and Latif, 1980). This avoidance behaviour becomes evident in areas where the human population has moved near nesting sites and built residences, resorts, military installations, airports and highways. Witham (1981) described the disruption of sea turtle nesting habitat through such human influences as increased construction (domestic, commercial and recreational), artificial lighting, physical barriers and vehicular traffic. He recommended mitigating management strategies such as transplanting eggs, shielding lights, removing barriers and restricting beach construction and use.

4.4 Mortality

4.4.2 Factors causing or affecting mortality

Hawksbill hatchlings are reportedly preyed upon by various species of crabs and fish, although other animals, such as birds, dogs, lizards, cats, are also undoubtedly

Table XXI

Mean reproductive rate of hawksbill turtles (data from tables 8 and 10, and section 3)[a/]

	Mean	Range	N
Clutch size	129	73-163	9
% eggs resulting in emerged hatchlings	81	71-91	4
Clutches/season	2-3	1-4	5
Hatchlings/female/season =	209-313		

a/ Mean figures for clutch size and percent eggs resulting in emerged hatchlings are weighted means of the means of populations with samples of 10 or more. The ranges are the ranges of the individual population means, and N is the number of populations with 10 or more samples

responsible for extensive hatchling mortality (see section 3.3.2). Starvation of hatchlings in oceanic environments, devoid of edible neuston, is an unknown and possibly large mortality factor.

Juvenile, subadult and adult hawksbills are preyed upon by large groupers, sharks and crocodiles (see section 3.3.4). Also individuals may stray into suboptimal environments, become stunned by low water temperatures and, eventually, die from thermal shock or starvation. These turtles are generally range extensions (see section 2.1).

Directed fishing mortality of juveniles, subadults and adult hawksbills in most locations is extensive (see section 5).

Hawksbill turtles (predominantly juveniles) are occasionally taken incidentally as a by-catch in other fisheries: Sumner (1909), Sumner, Osburn and Cole (1911), and De Sola and Abrams (1933) found specimens in pound nets on the eastern United States coast; Irvine (1947) found hawksbills in fishing nets in West Africa; Hughes (1969) reported a specimen from a shark net in southern Africa; Nietschmann (1972a, b) reported that hawksbills were frequently found suffocated in shrimp trawls in eastern Nicaragua; Jones and Fernando (1973) reported that hawksbills are occasionally captured in fish gillnets in India; Balazs (1977) found a specimen in a gillnet in Hawaii; Bullis and Drummond (1978) reported several captured in bottom trawls along the southeast coast of the United States; many are reportedly taken in shrimp trawls in the western Atlantic and Caribbean (Caribbean Conservation Corporation, 1980), and in the eastern Pacific (Cornelius, 1981; Green and Ortiz-Crespo, 1981) Hillestad et al., (1981) reviewed the worldwide incidental capture of sea turtles.

4.5 Dynamics of Population

There are no population models available for hawksbill turtles due to the lack of known biological parameters necessary for the appropriate calculations. However, McElroy and Alexander (1979) presented a hypothetical population model for hawksbills in the Solomon Islands, based on assumptions, which showed that there was a 1.17 percent probability of producing a nesting female from the total number of hatchlings produced in a nesting season.

4.6 The Population in the Community and the Ecosystem

The hawksbill turtle is a large circumtropical marine reptile which appears to exist in separate breeding populations (section 3.1). The hawksbill predominantly inhabits insular coral reefs, banks, lagoons, and estuaries adjacent to the nesting areas (section 2). It is an omnivore, feeding on a wide variety of organisms (section 3.4). Although hawksbills share their neritic habitat with several other species of sea turtles, as well as a myriad of fishes, there are no known serious competitors (section 3.2.3).

Hawksbill turtles are generally solitary nesters, rapidly laying eggs on isolated beaches; they have a tendency to renest two-three times in a season on the same beach, although some may renest on adjacent beaches. Hawksbills frequently nest on the same beaches as other species of marine turtles, but the actual nesting habitat is often divided either temporally or spatially; intergeneric mating is rare (section 2.4).

Hawksbill eggs and hatchlings are eaten by a variety of predators (sections 3.1.7 and 3.2.2), while juveniles, subadults and adults appear to be preyed upon predominantly by sharks (section 3.3.4).

Hawksbill populations are generally declining due to overexploitation (section 5.4) and nesting habitat destruction (section 4.3.2). Also, the effects of coral reef destruction, through pollution and construction, which reduces available foraging habitat, are unknown.

5. EXPLOITATION

5.1 Fishing Equipment and Methods

There are several basic methods of capturing hawksbill turtles used throughout the world, and these methods are used for the other sea turtle species as well. There are many modifications to these turtling methods and gear which are indigenous to local customs and several methods, or a combination of methods, may be utilized. Generally, the traditional fishing methods of harpoon, grapnel and remora are being replaced by the more efficient synthetic gillnets. The temperament of captured hawksbills is often pugnacious and fishermen must take precautions to avoid personal injury or excessive gear damage (see section 3.5.3).

Turtle turning: This is the method of turning over female turtles when they crawl onto the beach to nest. This method is practiced throughout the hawksbill nesting range as the major harvesting technique. No special gear is involved, although sometimes a stick is used for leverage. Because this methods selectively harvests reproductively active females, it is possibly the largest single factor in reducing hawksbill populations.

Harpoon: This method is one of the oldest methods of capturing hawksbills, although it is being replaced by the more efficient gillnet in many parts of the world. A harpoon consists of a wooden pole 4-5 m long with a 2-6 cm detachable steel point that has a strong line attached. When the turtle is

struck, the point becomes embedded in the carapace and the fishermen then pull the turtle into the boat after tiring it out. Turtles captured this way are particularly pugnacious and must be subdued with a club (see section 3.5.3). This method requires time patience and considerable skill, as the turtle must be found and struck before becoming alarmed and escaping. Copulating turtles are particularly susceptible to harpoon fishing because of their apparent preoccupation with mating.

Various harpooning techniques for hawksbill turtles have been used in the following locations:

Atlantic Ocean: De Bram (1773 fide De Vorsey, 1971), Bard (1855), Garman (1884), Nye (1887), Audubon (1926), Babcock (1937), Villiers (1958), Carranza (1962), Marquez (1965, 1976), Craig (1966), Carr, Hirth and Ogren (1966), Nietschmann (1971, 1972, a, 1974), Cardona and Rua (1972), Tovar (1973), Ross (1980).

Pacific Ocean: Seale (1911), McCarthy (1955), Trust Territories of the Pacific Islands (1957), Pritchard (1977), Spring (1979, 1981a), Onorio (1979), Uchida (1979, 1980), Cliffton, Cornego and Felger (1981), Kowarsky (1981), Vaughan (1981).

Indian Ocean: Hornell (1927), Deraniyagala (1939), Loveridge and Williams (1957), Frazier (1974, 1981a), Garnett (1978), Kar and Bhaskar (1981).

Illustrations of harpoon gear are found in the following sources: Caldwell (1963), Japanese Tortoise Shell Association (1973), Hughes (1973, 1976) and Uchida (1979).

Net: There are two types of net used to capture hawksbill turtles, the gillnet and the seine. The gillnet mesh is constructed of tree bark fibre, coconut fibre, cotton twine, nylon, or monofilament; the head rope is held afloat with wood, bamboo or plastic floats and the foot rope is held down with lead, stone or scrap iron. These gillnets range in length from 15 m to 180 m long by 3-4 m wide, with a mesh size ranging from 10 cm to 40 cm. In the Caribbean area, wooden decoys simulating female turtles are sometimes tied to the head rope to attract males. The nets, anchored near reef areas where hawksbills abound, are left to fish overnight. A single boat may set many nets in a single night, completely covering a reef. Sometimes these nets are not anchored overnight but are set near reefs during the day and turtles are driven into them by boats or swimmers. They are also used to surround turtles seen foraging on reefs during the day. Seines are constructed similarly to gillnets but have finer mesh sizes and are usually fished unanchored during the day by either surrounding observed turtles or by blocking off exits to lagoons which hawksbills frequent.

An interesting netting method used in the Cayman Islands, called a turtle trap, is described as a 1.5-m diameter iron ring with an attached net bag which is dropped over foraging hawksbills (Thompson, 1947).

Various netting techniques for hawksbill turtles have been used in the following locations:

Atlantic Ocean: Nye (1887), True (1887), Wilcox (1904), Schmidt (1916), Audubon (1926), Babcock (1937), Thompson (1945), Villiers (1958), Carranza (1962), Marquez (1965, 1976), Duke (1967), Nietschmann (1971, 1972, a, 1974), Cardona and Rua (1972), Ramos (1974), Thurston and Wiewandt (1976), Carr (1977), Ross (1980).

Pacific Ocean: Seale (1911), Le Poulain (1941), Trust Territories of the Pacific Islands (1957), Pritchard (1977), McElroy and Alexander (1979), Onorio (1979), Pita (1979), Spring (1979), Alcala (1980), Uchida (1980), Vaughan (1981).

Indian Ocean: Deraniyagala (1939), Valliappan and Pushparaj (1973), Jones and Fernando (1973), Hughes (1973), Shantharam (1975), Spring (1981a), Frazier (1981a).

Illustrations of netting gear are found in the following sources: Kuriyan (1950), Craig (1966), Travis (1967).

Diving: This method has several variations in techniques and gear. The fishermen may catch hawksbills by hand by either jumping off a moving boat onto the carapace of a surfaced turtle or by skin diving, which is particularly effective at night when the turtles are sleeping under coral ledges in shallow water. Spear guns and slings are becoming more popular, and are also more productive at night. Juvenile and subadult turtles are more likely to be captured by divers because large, thrashing adults are difficult to handle in the water. Unfortunately, speared adult turtles may escape to become killed by sharks or they may eventually die elsewhere from their wounds. A diving technique, apparently endemic to Japan's Ryukyu Islands, involves the use of 6-m bamboo poles which have short pieces of steel rod at the tip; a fish hook is wired to the steel tip and heavy line is tied to the eye of the hook. The diver then hooks a turtle in the neck, the pole slips out of the tip and floats to the surface, and the turtle is pulled in on the attached line (Hendrickson, 1965). A similar technique was introduced into Micronesia by the Imperial Japanese Armed Forces during World War II. An interesting diving technique to locate turtles is used by natives in the Palau District of Micronesia,

whereby experienced divers seek hollows under the coral where turtles frequently rest. A wooden stick with a line attached is wedged into the middle of the entrance. When a turtle enters the hollow, it dislodges the stick which floats to the surface and is seen by the fishermen from their canoes (Trust Territories of the Pacific Islands, 1957).

Various diving techniques have been used in the following locations:

Atlantic Ocean: True (1887), Marquez (1965, 1976), Nietschmann (1971, 1972a), Cardona and Rua (1972), Ramos (1974) Thurston and Wiewandt (1976), Carr (1977), Ross (1980).

Pacific Ocean: McCarthy (1955), Trust Territories of the Pacific Islands (1957), Japanese Tortoise Shell Association (1973), Pritchard (1977), McKeown (1977), McElroy and Alexander (1979), Onorio (1979), Pita (1979), Alcala (1980), Spring (1979, 1981a), Kowarsky (1981), Vaughan (1981).

Indian Ocean: Hughes (1976), Garnett (1978), Kar and Bhaskar (1981).

Remora : This is a very old method of turtle fishing practiced for centuries by natives around the world and was first described from Cuba by Columbus in 1494. The technique used is to fasten a line to the caudal peduncle of a remora (family Echeneidae) by a metal ring, band or simply a knot; the remora is then thrown overboard in the vicinity of a turtle. The fish then adheres to the turtle by the suction disc and is then pulled to the boat. The remoras are kept alive in pens or canoes filled with sea water, and they are well taken care of by the fishermen who fish them frequently and keep them for long periods of time. Presently, this method is rarely used, since more productive techniques have been introduced.

Remora turtling has been described in the following sources: De Sola (1932), Caribbean; Deraniyagala (1939), Sri Lanka; McCarthy (1955), Australia; Travis (1967), Somalia; Hughes (1973), Madagascar; Frazier (1981a), Kenya, Yemen.

Illustrations of remora turtling are found in Gudger (1919, a, b).

Grapnel: These devices are made from weighted fish hooks or curved, sharpened steel rods which are securely fastened to a central post, upon which a rope is fastened. The grapnel is dragged to the turtle, which is seen on the shallow ocean bottom, and is quickly jerked upwards when the hooks pass underneath it. The hooks thus, become embedded in the soft plastron or limb and the turtle is then pulled to the surface.

Grapnel turtling techniques have been described in the following sources: Nye (1887), Bahamas; Seale (1911), Philippines; Hughes (1973), Madagascar; Frazier (1981a), Kenya.

Illustrations of grapnel gear are found in the following source: Travis (1967), Somalia.

5.2 Fishing Areas

Hawksbills are fished throughout their tropical distribution (see section 2.1 and Figure 4), most being captured on reefs, banks and in lagoons adjacent to nesting beaches. Gillnets are fished in lagoon channels and passages between reefs, and harpooning for copulating turtles generally takes place in deeper water in front of nesting beaches. Diving, particularly at night for sleeping turtles, takes place on the shallow reef slopes facing deep oceanic depths.

5.3 Fishing Seasons

Hawksbill turtles are opportunistically harvested year-round wherever encountered. However, the majority of adult turtles are captured during the reproductive aggregations at the nesting beaches during the nesting season, the time of which varies with location (Table 2). At this time, copulating and nesting turtles are less wary, making them more susceptible to harvesting techniques.

5.4 Fishing Operations and Results

Hawksbill meat is generally eaten throughout its range, although the meat is often reported to be of poor quality, being dark and oily with a strong flavour. In spite of this, hawksbill meat is preferred over that of other sea turtles at Cayman Brac, San Andres and Old Providence Islands in the Caribbean Sea (Lewis, 1940; Thompson, 1947; Carr, 1956). The hawksbill is reportedly poisonous in many areas throughout its range, but often without documented cases. In many instances the hawksbill has been accused of being poisonous, possibly because of its strong flavour, which Carr (1956) believes to vary according to diet.

Hawksbills are not eaten, or are reluctantly eaten because of their reputed toxicity in the following locations: Gulf of Guinea (Greef, 1884), Australia (Musgrave and Whitley, 1926; Bustard, 1972), Sri Lanka (Deraniyagala, 1933), Gulf of Siam (Le Poulain, 1941), Colombia (Dunn, 1945), India (Acharji, 1950; Shantharam, 1975), Mauritius (Jones, 1956), New Guinea (Brongersma, 1958), Mexico (Del Torro, 1960), West Africa (Villiers, 1962), Seychelles (Frazier, 1971), Mauritius (Hughes, 1973, 1976), Senegal (Villiers, 1958; Maigret, 1977), Sudan (Hirth and Latif, 1980), Oman (Ross, 1981).

Documented cases of hawksbill turtle poisoning are relatively rare, having been reported from the following locations: Taiwan (Kinugasa and Suzuki, 1940), Gilbert Islands (Cooper, 1964; Onorio, 1979), Ryukyu Islands (Hashimoto et al., 1969; Hashimoto, 1979), Philippines (Ronquillo and Caces-Borja, 1960), Australia (Kowarsky, 1981), Solomon Islands (Vaughan, 1981), New Guinea (Romeyn and Haneveld, 1956; Spring, 1981, a), Sri Lanka (Deraniyagala, 1930, 1939), India (Valliappan and Pushparaj, 1973). Pillai et al., (1962) described in detail the clinical and pathological findings (including photomicrographs of affected epithelial, muscular, liver, kidney and heart tissues) of 130 cases of hawksbill poisonings in India.

Halstead (1978) reviewed the cases of turtle poisonings, summarizing all pertinent information. He found that poisoning was seasonally sporadic with a geographically intermittent distribution, and could result from eating either the meat, fat, viscera or blood. Symptoms generally appear from within a few hours to several days, depending upon amount ingested and the person. Major symptoms are: Nausea, vertigo, vomiting, diarrhea, severe gastric pain, sweating, coldness of the extremities, and a dry, burning sensation of lips, mouth and throat. Additionally, the tongue develops a white coating with tiny pustules, and victims may suffer from headaches and general lethargy. Halstead describes these clinical, as well as the pathological, characteristics in detail. There are no antidotes, consequently treatment is symptomatic. The overall case fatality rate is 28 percent, with the oldest and the youngest persons reportedly being more susceptible. Prevention is difficult, since toxic turtles are impossible to differentiate from non-poisonous turtles, the best method being to feed a sample to a dog or cat and wait at least 24 h. The origin of the toxin is unknown, but it is believed to be caused by ingestion of poisonous algae, jellyfish and even sea snakes (Deraniyagala, 1930, 1939; Le Poulain, 1941; Loveridge, 1946; Pillai et al., 1962; Villiers, 1962; Vaughan, 1981).

Indigenous people have attempted to identify toxic hawksbills by an interesting variety of methods. In Sri Lanka the fishermen offer bits of raw liver to crows - if rejected, the turtle is discarded; also, poisonous flesh reportedly turns greenish if mixed with slaked lime (Deraniyagala, 1930, 1939, 1953). Fishermen in India believe that the blood of toxic turtles thickens on a knife blade, and that a drop of blood on the skin will itch and become inflamed. They also believe, like the fishermen of Sri Lanka, that lime changes toxic meat greenish in colour (Valliappan and Pushparaj, 1973). Fishermen of the Suarkin Archipelago of Sudan choose a man who neither smokes nor drinks alcohol to taste the liver - if "evil-tasting", the meat is discarded (Hirth and Latif, 1980). Also, in the Solomon Islands, hawksbills that have unusually pale plastrons and short-straight intestines are believed to be poisonous and are not eaten (Vaughan, 1981).

Deraniyagala (1930, 1939) reported that if a toxic hawksbill should be eaten, the resulting sickness supposedly could be cured by dosing the patient with soup made from the carapace and plastron of Chelonia mydas.

Hawksbill eggs are eaten wherever and whenever found, apparently without any ill effects, being an important protein source (see section 1.3.3) in many lesser-developed villages. Calipee is also prepared for consumption in many parts of the world, and the oil and fat are commonly used for cooking.

The hawksbill turtle is most famous for the horny scutes called "tortoise shell", which are obtained from the carapace. There are 13 large and 25 small scutes on a turtle, and each scute has, when cleaned and polished, a rich brown mottling on a yellowish-translucent background. There are several different grades of shell depending on general colouration, the darker shell having the lowest demand and the lighter coloured or "blond" shells being the most often preferred. Articles such as dishes, knives, forks and spoons have been fashioned from hawksbill scutes since pre-historic man. However, the beauty of these scutes was quickly realized by affluent personages, and the manufacture of luxury items, such as the following, began: hair pins, combs, rings, nose rings, earrings, necklaces, brooches, fans, belts, miniature animals, inlayed furniture, and (more recently) eyeglass frames, cuff-links, tie tacks, buttons, snuff boxes, jewelery boxes, trays, model pagodas and model ships. The hawksbill turtle shell industry has thrived through the ages, dating back to ancient Greece, Rome and Egypt (Deraniyagala, 1939; Smith, 1958; Parsons, 1962; Schafer, 1962; Hughes, 1970; Hirth and Latif, 1980). European treasure ships returning from the New World were laden with turtle shell (Anon., 1980). Babcock (1940) presented a brief historical summary of the tortoise shell industry, as well as a state-of-the-arts profile, in the mid-twentieth century United States and Parsons (1972) gave an excellent historical account of the world-wide trade in hawksbill turtle shell.

Methods of scute removal are universally similar, the scutes being removed from the body carapace when the turtle is either dead or alive. More than one method may be used in any one location. The scutes on the carapace of a dead turtle are loosened when either placed in hot water (Seale, 1911; Hornell, 1927; Deraniyagala, 1939; Loveridge, 1946; México, Secretaría de Industria y Comercio, 1966; Hughes, 1971) or buried in the sand for a week or two (Seale, 1911; Deraniyagala, 1939; Loveridge, 1946; Travis, 1967; Ubeda, 1973). Removing scutes from

live animals is accomplished by passing a torch over the carapace or by suspending the turtle upside down over a fire (Bard, 1855; Shelford, 1917; Deraniyagala, 1939; Loveridge, 1946; Larrea, 1948; Domantay, 1952-53; Roze, 1955; Parsons, 1956; Hirth and Carr, 1970; Moore and Balzarotti, 1976). These turtles are released alive and are believed to regenerate new scutes, although they are reportedly thinner than the original scutes. Deraniyagala (1939) provided evidence that scute regeneration takes place, and Uchida (1980) reported the capture of several specimens with thin, regenerated scutes.

The amount of shell from each adult turtle varies with age and size from 1 kg to 6 kg; the average weight reported from 12 sources in the literature is 3.3 kg. Scute yield between nesting populations probably also varies due to the differences of mean sizes of nesting turtles (Table III). Also, there are unsubstantiated reports in the older hawksbill literature that the female turtles have much thicker carapace scutes than the males.

The scutes are cleaned and then cut into the proper sizes and shapes with a fine-tooth saw. Additional shaping is done by first softening the shell in hot water and then moulding it into the desired shape. Several scutes may be joined together by clamping them together and immersing them in hot water. Also, the sawdust shavings of the scutes are heated and then moulded into desired articles. Care is taken with the shell, however, because it darkens and opaques under excessive heat. Descriptions of working shell are found in the following sources: Dumeril and Bibron (1835), Villiers (1958), Pufahl (1915), Tressler and Lemon (1951), Smith (1958), Krefft (1962) and Webster (1972).

Whole carapaces of juveniles and some adults are cleaned, polished and sold for wall hangings, and juvenile turtles are also stuffed and sold as tourist souvenirs. Other products from harvested hawksbills include leather, oil, perfume and cosmetics.

Hawksbills of all sizes appear to be universally harvested whenever found (see all references in this section), and this has led to drastic world-wide population decreases (Carr, 1969), with the populations from Australia and the Arabian Peninsula as exceptions. Mackey (1980) and King (1981) described the overexploitation situation that world-wide hawskbill populations now face.

Many ancient beliefs have surrounded the hawksbill turtle, particularly in the tropical Pacific islands. The scutes were used for medicinal purposes in Hawaii (Balazs, 1977), and for ceremonial "women's money" in Palau (Helfman, 1968). In Yap, it is believed that burning a hawksbill shell causes leprosy, hence the word for hawksbill turtle and leprosy are the same (Trust Territory of the Pacific Islands, 1957). In pre-Christian Satawal, the hawksbill was considered sacred (McCoy, 1974), and hawksbills in the Gilbert Islands are family totems and, as such, are considered sacred (Cooper, 1964; Onorio, 1979). Spring (1981a) described the special socio-economic significance that sea turtles (including hawksbills) have in Papua New Guinea, and some of the traditional rules and rituals associated with the turtle hunting.

National catch statistics for hawksbill turtles usually reflect the amount of shell produced; items such as stuffed juveniles, leather, jewelery, are not traceable to the country of origin. Japan is the largest importer of stuffed hawksbills and shell, turtles traditionally being a sign of good luck and longevity; the largest supplies come from Panama, Cuba, Indonesia, Singapore, Philippines, Kenya, Tanzania, Nicaragua and the Cayman Islands (Uchida, 1977). Summaries of national statistics are available from the following countries: Philippines (Seale, 1917; Domantay, 1968; De Celis, 1981), Seychelles (Frazier, 1971), Madagascar (Hughes, 1973), Mexico (Ramos, 1974; Marquez, 1974, 1976), Solomon Islands (McKeown, 1977; Vaughan, 1981), Japan (Uchida, 1977, imports only), Indonesia (Polunin and Sumertha, 1981). Regional import-export statistics are presented for Indonesia (Japanese Tortoise Shell Association, 1973; Kajahira and Uchida, 1974), and the western central Atlantic Ocean (Rebel, 1974). Additionally, world-wide statistics, broken down by country, are presented by Cato, Prochaska and Pritchard (1978) and Mack, Duplaix and Wells (1981).

6. PROTECTION AND MANAGEMENT

6.1 Regulatory Measures

Dating back to the nineteenth century, the literature contains many articles calling for conservation legislation and/or artificial hatching and rearing programmes in areas where hawksbill populations have been depleted due to overexploitation. Also, regulatory measures have recently been imposed on the capture and marketing of hawksbills in many nations in order to maintain healthy and stable breeding populations. Because these laws are numerous and often complex, they are not individually discussed here. Legislation to protect against nesting habitat destruction is, however, almost non-existent at this time. Major legislative actions involving hawksbills are described for the following locations: Australia (Bustard, 1969), Sabah (De Silva, 1969, a), Ghana (Anon., 1971), Sri Lanka (Anon., 1972), Seychelles (Frazier, 1974, 1979a; Salm, 1976). There is also the United States Endangered Species Act of 1973 which makes it unlawful to take, import or export hawksbill turtles or products. Regulatory measures for many nations in the western central Atlantic Ocean are summarized by Rebel

(1974), Bacon (1975, 1981) and Caribbean Conservation Corporation (1980); additional regulations for sea turtles in various countries around the world may be found in Pritchard (1969b), IUCN (1969, 1971), Hirth (1971b) and Björndal (1981).

The reduction of hawksbill populations around the world, due to overexploitation, has prompted the International Union for Conservation and Natural Resources to list the hawksbill turtle an endangered species (IUCN, 1968, 1970, 1975). An international agreement prohibiting members from commercially exporting or importing any sea turtle products was drawn up and signed by many nations at the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (IUCN, 1973). Carr and Maylan (1980) felt that, because of the recent large importation figures of hawksbill shell, the only hope for the survival of the hawksbill species is through effective enforcement of CITES.

Enforcement of these various national and international regulatory measures is difficult, and hawksbills of all sizes are often harvested wherever and whenever encountered because local police forces may be logistically unable or unwilling to enforce legislation concerning local turtle fisheries. The complicated legal aspects of national and international sea turtle conservation legislation is presented by Navid (1981), and the myriad problems of law enforcement are discussed by Gomez (1981) and Bavin (1981).

6.2 Management Strategies

The survival situation of the overexploited world-wide hawksbill turtle populations is somewhat tenuous. Carr (1972) and Carr and Meylan (1980) felt that the hawksbill's solitary nesting on small scattered beaches made it impossible to adequately protect nesting turtles and nesting habitat. However, in spite of several outlined conservation problems, Hendrickson (1981) felt that the hawksbill may be the most likely species of sea turtle to survive because of its scattered, opportunistic nesting behaviour. Carr and Stancyk (1975) believed that the species must be regarded as being composed of many individual breeding/nesting populations (such as appears to exist at Torres Strait) in order to be effectively managed, arguing that genetically distinct demes could otherwise be overlooked before they are eradicated.

Sea turtle conservation strategies are varied, generally revolving around one or more of the following elements: habitat protection/improvement, egg hatcheries, head-starting, transplantation, protective legislation, regulation of international trade, gear development to reduce incidental mortality in other fisheries, and improved public education. Habitat protection/improvement pertains to nesting beach habitats and forage habitats; this method consists of such elements as restricted beach construction and usage, the clearing of beach obstacles such as rocks and vegetation, and the restriction of reef blasting and dredge and fill operations. In egg hatcheries, transplanted eggs are incubated in artificial nests and the hatchlings immediately released at sea; thereby reducing egg and hatchling mortality from tides, man and beach predators. Head-starting is the rearing of hatchling turtles incubated in egg hatcheries for periods of several months to a year or more before their release in the wild. This procedure reduces hatchling mortality from beach and oceanic predators. Transplantation consists of transplanting either eggs or newly emerged hatchlings to beaches where it is hoped they will imprint on the beach and return as adults to nest. This is probably the least effective management strategy, because of the apparent failures of all such projects. Protective legislation may be an integral part of, or may influence all sea turtle management strategies; the effectiveness being dependent upon the enforceability of the legislation. Regulating international trade of sea turtle products by multilateral agreements hopefully will reduce the market for sea turtle products, and subsequently lower the directed harvesting effort. Gear development to reduce the number of sea turtles caught incidentally in other fisheries, particularly the shrimp trawl fishery, has proceeded in the United States with satisfactory results (NOAA/NMFS, 1981). The effectiveness of these gear developments on a global basis is dependent upon the availability of these developments to other nations, and their willingness to use them. Effective public education to promote conservation awareness for sound resource management is possibly the most important, yet most overlooked, sea turtle management tool, particularly in lesser developed nations. However, all turtle conservation efforts are negated if the local people do not respond positively to sound, culturally sensitive public education programmes. The advantages and disadvantages of the sea turtle management strategies listed above are discussed in detail by Dodd (1978, 1981), Pritchard (1980, 1981b), Ehrenfeld (1981), Reichart (1981) and Shabica (1981). Descriptions of conservation strategies adopted in various countries are presented in Björndal (1981).

6.3 Artificial Stocking

Artificial stocking is thought to reduce predation on eggs, hatchlings and juveniles, there being two basic methods used:

(1) egg hatcheries, the transplanting of eggs to artificial nests for incubation and subsequent immediate release of the hatchlings, and

(2) head-starting, the retention of turtles for periods up to a year before release.

Hawksbill eggs are transplanted to egg hatcheries for incubation in Sabah (De Silva, 1968, 1969, a, b, 1971; Uchida, 1979, 1980), and Grenada (Goodwin, 1980, 1981). Head-starting projects have been reported from the following locations: Micronesia (Trust Territories of the Pacific Islands, 1957; McVey, 1972; Anon., 1972a; Pritchard, 1977), Western Samoa (Witzell, 1972, 1974), Solomon Islands (Vaughan, 1981), Australia (Bustard, 1973, 1974; Carr and Main, 1973; Uchida, 1974). The methods, foods and diseases involved in head-starting hawksbill turtles are similar to those for turtles reared for eventual harvest (see section 7). Artificial stocking by these methods has been criticized by some biologists who argue that certain biological parameters, such as clutch sex ratio and imprinting behaviour, may be unnaturally affected, and that these techniques have not been proven to be effective. See also section 6.2.

7. MARICULTURE

Hatchling hawksbills are reared in captivity for several months in order to supply juvenile turtles for stuffing as curios, and they are also raised for several years to provide scutes for tortoise shell. Some of the rearing projects, particularly in Micronesia and Australia, were designed to head-start a small percentage of juvenile turtles for conservation purposes. The major rearing projects have been described in the following sources: Le Poulain (1941), Trust Territories of the Pacific Islands (1957), Japanese Tortoise Shell Association (1973), Carr and Main (1973), Uchida (1974, 1979, 1980), Sumertha (1976). In addition, Smart (1973) studied the organization, management and marketing prospects of the Australian farming venture described by Carr and Main (1973).

The turtles are generally reared in small concrete ponds; wooden, plastic, or metal tanks; or sections of fenced-off lagoon, or estuarine areas. Water exchange is by pump, bucket or tidal flow, depending on the type of holding pen and the affluence of the farmer. The rearing pens are often partially shaded from intense, direct sunlight to reduce algal growth.

Captive hawksbill turtles will eat almost any kind of fish, mollusc or crustacean, as well as some varieties of sea urchins and jellyfish, occasionally nibbling at algae or sea grasses. However, reared turtles grow faster on a high protein diet and are usually fed chopped fish. McVey (1972) reported a food conversion ratio of 3:1 in young captive Micronesian hawksbills fed fish.

The behaviour of hawksbills reared in captivity is often aggresive; they frequently bite each other, particularly during feeding (see section 3.5.3). The frequency of biting is probably related to the stocking density and the feeding method; increased biting occurs in overcrowded conditions with localized feeding.

Disease is a common problem with most rearing operations, generally being aggravated by poor water circulation and by the wounds resulting from the continual flipper nipping. The most common malady is a highly infectious, fatal, fungus-like disease which erodes the eyes, neck and wounded flippers. Turtles raised in crowded tanks under poor rearing conditions can quickly become infected, suffering massive mortalities in only a few days (Hornell, 1927). This is a very rapidly developing pathogen which has been successfully treated in the early stages by topical application of gentian violet. Carr and Main (1973) also noted abnormal posterior buoyancy accompanied by cloacal swelling, and high nematode infestation originating from the spotted herring food source.

Hawksbill turtles, reared in fairly stagnant or shallow water, may become covered with algae. Although not considered pathogenic, this algae could be deleterious to the overall health of the turtles and is often scrubbed off on a regular basis.

It is believed that hawksbills will develop lighter coloured (hence more valuable) shells if raised in relative darkness in covered pens (Le Poulain, 1941), or that rearing in fresh water will enhance the shell colour (Brown, 1908; Japanese Tortoise Shell Association, 1973).

Although it appears that hawksbill turtles can be successfully raised in captivity, optimal rearing conditions, such as stocking density, holding structure size and construction, water exchange rate, feeding rate and disease control are not known.

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